

DINOFLAGELLATE CYSTS FROM THE BRACKLESHAM BEDS (EOCENE) OF THE ISLE OF WIGHT, SOUTHERN ENGLAND

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ABSTRACT

Dinoflagellate cysts considered to be indigenous to the Eocene are described from the Bracklesham Beds (Lower, Middle and Upper Eocene) of the Isle of Wight, southern England. A total of 106 taxa are recorded, including three new genera: *Achilleodinium*, *Araneosphaera* and *Distatodinium*, and 23 new species: *Araneosphaera araneosa*, *Areoligera sentosa*, *A. tauloma*, *A. undulata*, *Cyclonephelium spinetum*, *C. vicinum*, *Distatodinium craterum*, *Heteraulacacysta* ? *leptalea*, *Homotryblium abbreviatum*, *H. oceanicum*, *Hystrichokolpoma granulata*, *H. salacia*, *Hystrichosphaeridium asterium*, *Impletosphaeridium cracens*, *I. insolitum*, *I. luxurium*, *Kisselevia insolens*, *Lanternosphaeridium vectense*, *Phthanoperidinium alectrolophum*, *P. echinatum*, *P. tritonium*, *Turbiosphaera galatea* and *T. magnifica*. Five informal microplankton zones are defined for the Bracklesham Beds, based on the stratigraphical ranges of 70 dinoflagellate cyst species. The Bracklesham Beds at Whitecliff Bay and Alum Bay, Isle of Wight, are correlated using the microplankton zones. The recorded microplankton assemblages are compared with those described from the Lower Eocene of the London Basin and the Eocene of northern Europe. The most significant palynostratigraphical features of the recorded assemblages are listed and discussed in relation to microplankton assemblages from Palaeogene sediments throughout the world.

I. INTRODUCTION

THE investigation of organic-walled microplankton (dinoflagellate cysts and acritarchs) from Palaeogene sediments in southern England has been conducted at Sheffield University under the supervision of Dr Charles Downie. Following the thesis work of Williams (1963) on the Lower Eocene London Clay of the Hampshire and London Basins, and Husain (1967) on the Palaeocene and Lower Eocene of the

London Basin, the present author has studied the Bagshot and Bracklesham Beds of the Isle of Wight in the Hampshire Basin where these sediments succeed the London Clay and include representatives of the Lower, Middle and Upper Eocene.

This study had two main objectives, to record and describe the organic-walled microplankton in these sediments, and to evaluate their potential for stratigraphical correlation.

The Bagshot Sands proved to be palynologically barren, but the Bracklesham Beds yielded rich assemblages of organic-walled microplankton, pollen and spores. The microplankton include dinoflagellate cysts which are considered to be indigenous to the Bracklesham Beds, reworked dinoflagellate cysts derived from Jurassic and Cretaceous sediments, acritarchs (including both indigenous and reworked forms), and members of the Chlorophyceae and Prasinophyceae. In this paper only the indigenous dinoflagellate cysts are described.

All type and figured specimens with a British Museum (Natural History) slide number quoted in this paper are lodged in the palaeontological collection of the British Museum (Natural History), London. Several of these specimens were figured in Eaton (1971a) where they were described as being housed in the Micro-palaeontology Laboratory, Department of Geology, The University, Sheffield, Yorkshire, England. The original slide numbers in Eaton (1971a) and the corresponding British Museum (Natural History) slide numbers in this paper are :

W40.1.	V.57756	AB5.2.	V.57778
W51.1.	V.57759	AB28.1.	V.57788
W51.C1.	V.57760	AB40.1.	V.57790
W54.C1.	V.57761	AB40.2.	V.57791
W56.1.	V.57763	AB40.C1.	V.57794
W56.2.	V.57764	AB40.C2.	V.57795
W56.C1.	V.57766	AB42.C1.	V.57798
W58.1.	V.57770	AB44.4.	V.57802
		AB44.C1.	V.57803

II. STRATIGRAPHY

Palaeogene sediments in southern England are essentially restricted to the Hampshire and London Basins (Fig. 1). These two areas are now structurally separated, but there is no evidence this was so during the Palaeogene, when they were both situated in the Anglo-Paris-Belgian depositional basin.

Eocene sediments outcrop in a narrow strip running east to west across the Isle of Wight from Whitecliff Bay to Alum Bay (Fig. 2). At these two localities the five main lithostratigraphical units of the Eocene are exposed in cliff sections: the basal Reading Beds resting on the eroded upper surface of the Chalk are succeeded by the London Clay, the Bagshot Sands, the Bracklesham Beds and the Barton Beds. At both localities the Bracklesham Beds are perfectly exposed in a vertical or near vertical attitude, and display a considerable variety of marine and non-marine sediments: sands, clays and sandy clays frequently yielding marine mollusca and foraminifera; laminated beds consisting of alternating layers of sand and clay, with carbonaceous matter occurring in thin seams or scattered on the bedding

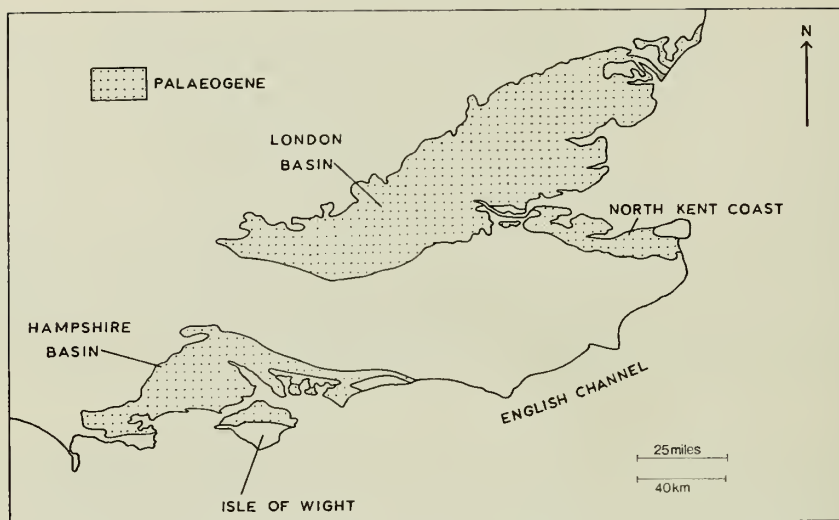


FIG. 1. Map showing the major outcrops of Palaeogene sediments in southern England.

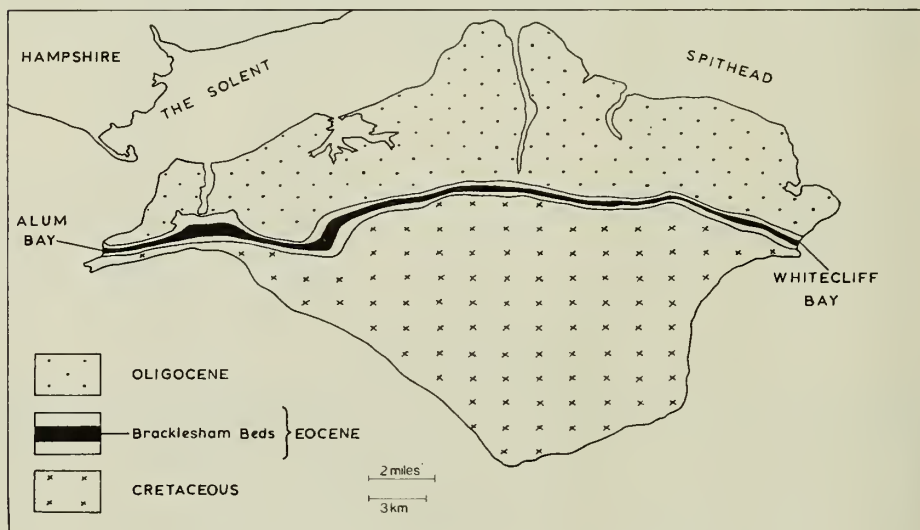


FIG. 2. Generalized geological map of the Isle of Wight.

planes; brightly coloured barren sands which are typically cross-bedded; pebble beds, non-marine clays, pipeclays and lignite beds.

At Whitecliff Bay the type section of the Bracklesham Beds (Fisher 1862) is 182 m (598 ft) thick and consists mainly of sands, clays and sandy clays yielding a marine fauna, and laminated beds (Fig. 3). The minor differences between Fisher's interpretation of the lithological divisions within the Bracklesham Beds and that of the author are mainly due to variations in the degree of exposure in the section.

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Bay and Alum Bay, Isle of Wight, with sample positions and sample productivity.

ALUM BAY

PRESTWICH 1846 & 1847		THIS STUDY		SAMPLE POSITION & PRODUCTIVITY
WHITE 1921		LITHOLOGICAL DIVISIONS	LITHOLOGY	

WHITECLIFF BAY

CURRY ET AL 1969		THIS STUDY		SAMPLE POSITION & PRODUCTIVITY
FISHER 1862		LITHOLOGICAL DIVISIONS	LITHOLOGY	

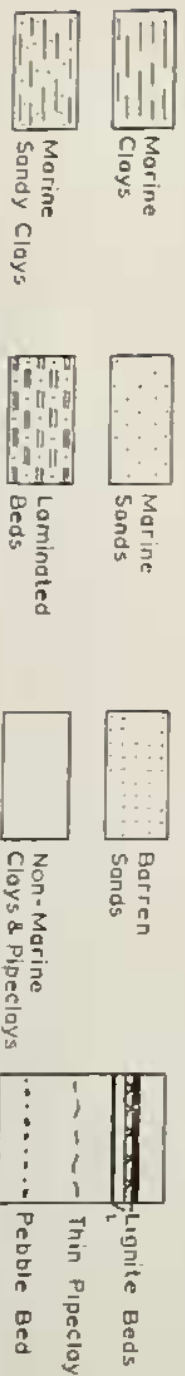
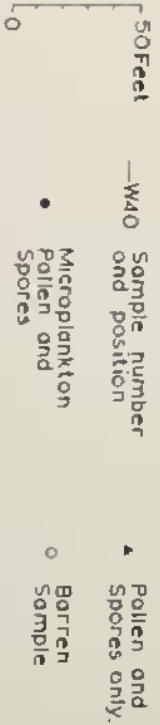
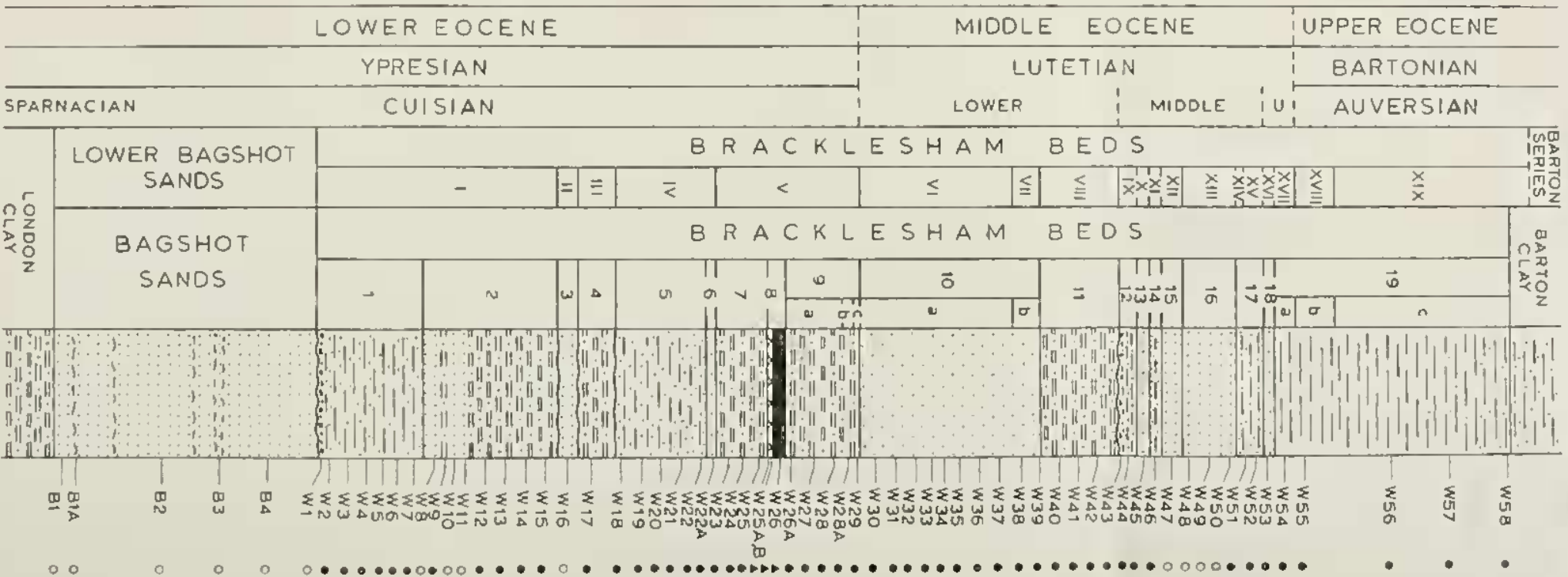
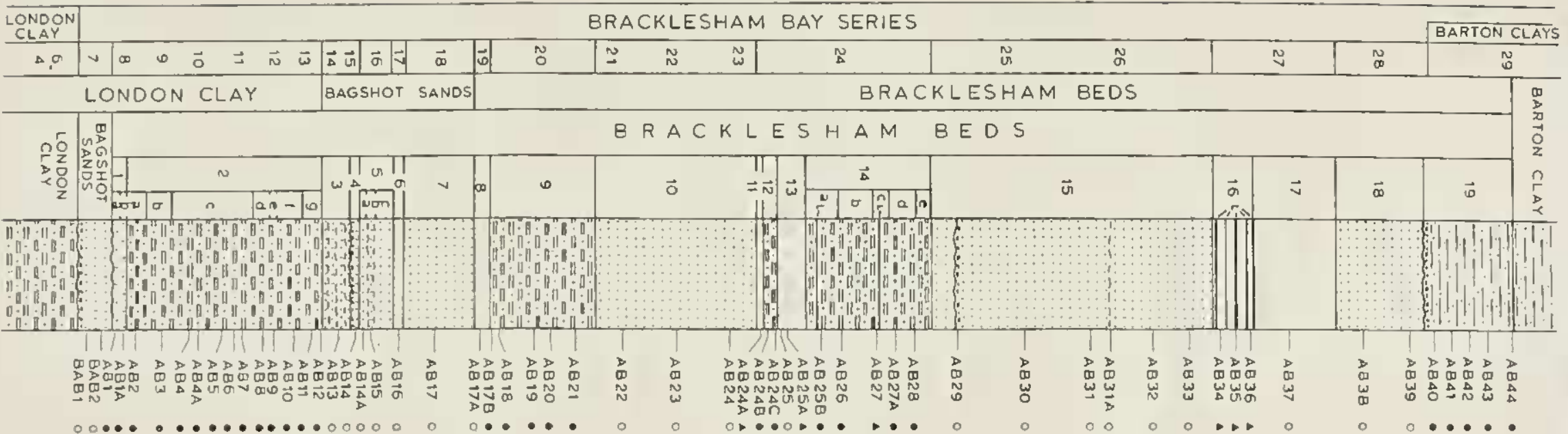


FIG. 3. The sections of the Bagshot Sands and the Bracklesham Beds exposed at Whitecliff Bay and Alum Bay, Isle of Wight, with sample position and sample productivity.

At Alum Bay the Bracklesham Beds are here considered to be 242 m (793 ft) thick and consist mainly of barren sands and laminated beds (Fig. 3). The positions of the top of the London Clay and the base of the Bracklesham Beds used in this study differ from the previously accepted interpretation (White 1921) in that the upper part of the London Clay of White is here assigned to the Bracklesham Beds, and the Bagshot Sands are represented by 6.1 m (20 ft) of grey and yellow sands. Apart from the inclusion of the Bagshot Sands this revised interpretation is comparable to Prestwich's concept of the London Clay and the Bracklesham Bay Series (Prestwich 1847). All interpretations of the latter part of the Alum Bay sequence are essentially based on lithological comparison with other sections. My lithological divisions within the Bracklesham Beds at Alum Bay have yet to be formally described, but they can be interpreted in terms of Prestwich's original subdivision of the sequence (Prestwich 1846).

The age of the Bracklesham Beds has been determined by comparing the marine faunas of mollusca and foraminifera in the Whitecliff Bay section with faunas from the Eocene of France and Belgium. The application of the French and Belgian stages to the Bracklesham Beds is discussed by Curry, Gulink & Pomerol (1969), and their interpretation is used here. The recognition of the Cuisian is based on the record of *Nummulites planulatus* in bed 5 (Fisher bed IV) by Wrigley & Davis (1937). Although there is no palaeontological evidence, they also assigned the Bagshot Sands and beds 1-4 (Fisher beds I-III) of the Bracklesham Beds to the Cuisian, but left the upper limit as indefinite. Between the horizon yielding *N. planulatus* and the greensands yielding *N. laevigatus*, there is an interval devoid of marine faunas (beds 7-9, Fisher bed V). Curry *et al.* consider this to represent the youngest part of the Cuisian. The recognition of the Lutetian is based on the presence of *N. laevigatus* in beds 10 and 11 (Fisher beds VI-VIII) and *N. variolarius* in beds 11-19a (Fisher beds VIII-XVII). The assignment of the highest Bracklesham Beds (bed 19b-c, Fisher beds XVIII and XIX) to the Auversian is based on faunal evidence from equivalent sediments at Huntingbridge, Hampshire.

The upper limit of the Bracklesham Beds is taken immediately below a horizon rich in *N. prestwichianus* which marks the base of the Barton Beds.

The Bracklesham Beds and the Bagshot Sands at Whitecliff Bay and Alum Bay were sampled for palynological study. All samples were prepared using the standard acid digestion technique. The sampled horizons and their palynological productivity are indicated in Fig. 3.

III. SYSTEMATIC DESCRIPTIONS

The 106 dinoflagellate cyst taxa recorded in this study and described in this section are assigned to three informal groups: the Gonyaulacacean and Peridiniacean Groups as described by Wall & Dale (1968a), and the Unknown Affinities Group for taxa not assignable to the two main groups. This procedure follows that adopted by Davey & Verdier (1971). The genera in each group are described in alphabetical order. In the systematic descriptions under 'DIMENSIONS', *n* indicates the number of specimens measured. The paragraph headed 'OCCURRENCE' includes

the stratigraphical distribution of the species in the Bracklesham Beds of the Isle of Wight, quoted in terms of Lower, Middle and Upper Eocene. In the paragraph headed 'PREVIOUS RECORDS' an asterisk (e.g. De Coninck 1972*) indicates a listed record of the species without description or illustration.

Division *PYRRHOPHYTA*

Class *DINOPHYCEAE*

Order PERIDINIALES

GONYAULACACEAN GROUP

Genus *ACHILLEODINIUM* nov.

DERIVATION OF NAME. From Achilles, Greek hero of the Trojan War.

DIAGNOSIS. Dinoflagellate cysts having a spherical or subspherical body bearing two types of intratabular processes: cylindrical processes, one per reflected plate area, hollow, circular to polygonal in cross-section, distally open or closed, variable in size; the larger processes occurring on the pre- and postcingular and antapical zones, the smaller on the apical zone. Slender processes, simple or bifurcate, distally open, restricted to the cingular and sulcal zones. Reflected tabulation 4', 6'', 6c, 5''', 1p, 1''''; archaeopyle precingular, formed by displacement of plate 3''.

TYPE SPECIES. *Hystrichosphaeridium biformoides* Eisenack 1954; Upper Eocene, East Prussia.

REMARKS. *Achilleodinium* n. gen. is similar to *Hystrichokolpoma* Klumpp 1953 emend. Williams & Downie 1966a and *Florentinia* Davey & Verdier 1973 in both overall morphology and reflected tabulation. *Hystrichokolpoma* is distinguished by having an apical tetratabular archaeopyle. In *Florentinia* the archaeopyle is formed by displacement of precingular plate 3'' with breakage or displacement of the apical plates. In *Achilleodinium* the archaeopyle is formed exclusively by displacement of plate 3'', and there is no breakage or displacement of the apical plates.

***Achilleodinium biformoides* (Eisenack 1954) n. comb., emend. herein**

Fig. 4; Pl. 1, figs 1-6

- 1954 *Hystrichosphaeridium biformoides* Eisenack: 68; pl. 11, figs 16-20.
- 1963 *Baltisphaeridium biformoides* (Eisenack) Downie & Sarjeant: 91.
- 1965 *Hystrichokolpoma biformoides* (Eisenack) Eisenack: 151; pl. 14, fig. 2.
- 1965 *Hystrichokolpoma biformoides* (Eisenack) Rozen: 22; pl. 3, figs 1-2; text-fig. 19.
- 1966a *Hystrichokolpoma biformoides* (Eisenack) Morgenroth: 28; pl. 6, figs 9-10.
- 1967 *Hystrichokolpoma* sp. [? *H. biformoides* (Eisenack)] Cookson & Cranwell: 206; pl. 1, fig. 11.
- 1967 *Hystrichokolpoma biformoides* (Eisenack) Morgenroth; Agelopoulos: 40; pl. 13 figs 5-6.
- 1972 *Hystrichokolpoma cinctum* Klumpp; Benedek: 28; pl. 9, fig. 7; not pl. 8, fig. 8.

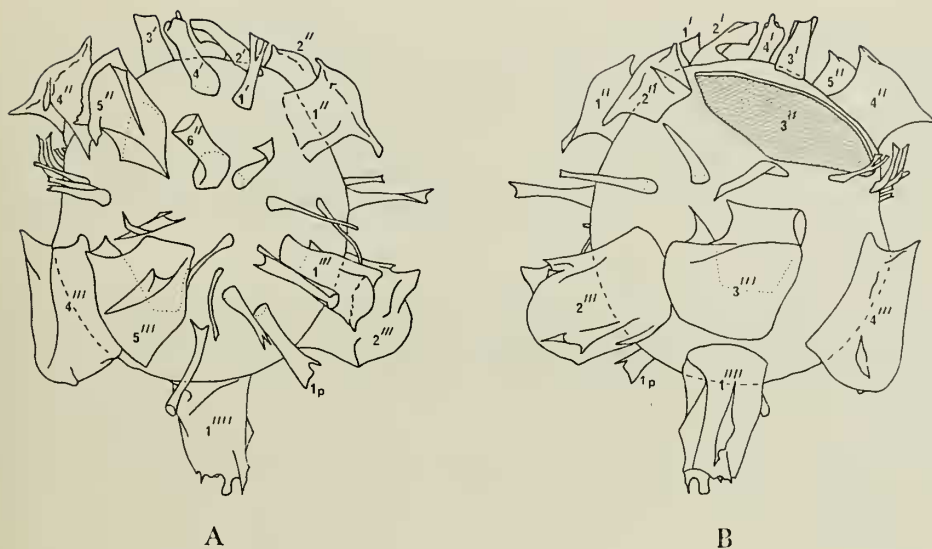


FIG. 4. *Achilleodinium biformoides* (Eisenack 1954) n. comb., emend., reflected tabulation. A. Ventral view. B. Dorsal view. The precingular archaeopyle (3'') is indicated by shading. V.57759 (12); W51.

EMENDED DIAGNOSIS. Cyst body spherical or subspherical with a smooth or finely granular surface. Processes intratabular, variable in size and shape, with a striated or finely fibrous appearance. Apical processes relatively narrow, typically open distally. Precingular processes 1''–5'', and postcingular processes 2'''–5''', are large, broad, circular to polygonal in cross-section, and usually distally expanded and closed. Processes 6'' and 1''' are relatively reduced. Cingular processes are slender, hollow, distally open, usually two, but sometimes one per reflected plate area. Sulcal processes similar to those on the cingular and apical zones. Antapical process usually longer than the other large processes. Reflected tabulation 4', 6'', 6c, 5''', 1p, 1''''; archaeopyle precingular, formed by displacement of plate 3''.

HOLOTYPE. The specimen figured as *Hystrichosphaeridium biformoides* by Eisenack (1954: pl. II, fig. 18), Upper Eocene, East Prussia.

DIMENSIONS. Holotype: overall diameter 70 μ ; diameter of cyst body 50 μ . Observed range: diameter of cyst body 42–63 μ ; large processes, length up to 22 μ , breadth up to 28 μ ; length of slender processes up to 17 μ . (n = 14).

REMARKS. The large processes frequently exhibit longitudinal folds, spines or tubules on the distal margin, and broad fenestrations at the proximal margin of the process wall. The distal margin in the open processes may be expanded, is irregular and often deeply incised. In some processes the incision extends to the proximal margin (Fig. 4A). Reduced precingular process 6'' is similar to the apical processes. Reduced postcingular process 1''' is similar to the precingular processes. The other

postcingular processes are usually larger than the precingular processes. Although the antapical process is usually the longest, it may be relatively narrow; its spines or tubules may be developed towards, but not actually at the distal margin. The specimen of *A. biformoides* figured by Morgenroth (1966a: pl. 6, figs 9–10) has an antapical process considerably longer ($40\ \mu$) than in specimens observed in this study. The overall range of form of the processes readily distinguishes *A. biformoides* from described species of *Hystrichokolpoma*, when its precingular archaeopyle is not exhibited.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Morgenroth 1966a; (?) De Coninck 1972*, questionably as *Hystrichokolpoma ? biformoides*) and of north Germany (Morgenroth 1966a); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); Upper Eocene of Belgium (Rozen 1965), of East Prussia (Eisenack 1954, 1965) and of north Germany (Agelopoulos 1967); Eocene, undifferentiated, of Chile (Cookson & Cranwell 1967, questionably as *Hystrichokolpoma* sp.); Middle and Upper Oligocene of north Germany (Benedek 1972, pl. 9, fig. 7 only).

Genus *ACHOMOSPHERA* Evitt 1963

Achomosphaera ramulifera (Deflandre) Evitt 1963

Pl. 1, fig. 7

- 1937 *Hystrichosphaeridium ramuliferum* Deflandre: 74; pl. 14, figs 5–6; pl. 17, fig. 10.
1963 *Achomosphaera ramulifera* (Deflandre) Evitt: 163, text-fig. 2.

DIMENSIONS. Observed range: diameter of cyst body $31\text{--}50\ \mu$; length of processes up to $22\ \mu$. ($n = 17$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Cretaceous, Albian (Davey & Verdier 1971), to Pliocene (Habib 1971); probably world-wide in distribution.

Achomosphaera alcornu (Eisenack) Davey & Williams 1966a

Pl. 1, fig. 11

- 1954 *Hystrichosphaeridium alcornu* Eisenack: 65; pl. 10, figs 1–2; text-fig. 5.
1966a *Achomosphaera alcornu* (Eisenack) Davey & Williams: 50; pl. 5, fig. 3.

DIMENSIONS. Observed range: cyst body $52 \times 42\ \mu$ to $70 \times 62\ \mu$; length of processes up to $30\ \mu$. ($n = 16$).

REMARKS. This species is morphologically similar to *Spiniferites pseudofurcatus* (Klump) Sarjeant 1970, and is distinguished by the absence of plate boundaries on the cyst body.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene of north Germany (Gocht 1969) and of northern Spain (Caro 1973); Lower Eocene of Belgium (De Coninck 1965, 1967*, 1968), of northern France (Gruas-Cavagnetto 1968, 1970b*), of north Germany (Gocht 1969), of northern Spain (Caro 1973) and of the Hampshire and London Basins in southern England (Davey & Williams 1966a; Downie, Husain & Williams 1971); Middle Eocene of north Germany (Agelopoulos 1967, Gocht 1969); Upper Eocene of Belgium (Rozen 1965), of East Prussia (Eisenack 1954) and of north Germany (Agelopoulos 1967); ? Upper Eocene of north Germany (Gocht 1969); Eocene, undifferentiated, of the eastern seaboard, U.S.A. (subsurface, offshore, Habib 1972) and of Romania (Balteş 1969, as *Perisseiasphaeridium pannosum*); Middle Oligocene of north Germany (Gerlach 1961, Gocht 1969, Benedek 1972); Upper Oligocene of north Germany (Benedek 1972); ? Middle Miocene of north Germany (Gerlach 1961).

Achomosphaera membraniphora (Agelopoulos 1964) n. comb., emend. herein

Fig. 5; Pl. 1, figs 8–10

1964 *Hystrichostrogylon membraniphorum* Agelopoulos: 674; figs 1–2.

EMENDED DIAGNOSIS. A smooth unornamented species of *Achomosphaera* in which the periphragm is separated from the endophragm at the antapex and over the ventral surface, forming a distinct pericoel in this region. The processes developed over the area of the pericoel are shorter than the other processes present on the cyst body.

DIMENSIONS. Observed range: diameter of cyst body 28–48 μ ; height of pericoel 6–20 μ ; length of processes up to 24 μ . (n = 18).

REMARKS. In process form and distribution, and archaeopyle position, *A. membraniphora* is directly comparable to the typical Palaeogene form of *Achomosphaera ramulifera*, and is only distinguished by the development of the pericoel. Agelopoulos (1964, 1967) described this form as the type species of *Hystrichostrogylon*, and he considered the archaeopyle to be apical in position. His illustrations show lateral views of several specimens, and in this orientation a precingular archaeopyle can appear to be apical – compare with the illustrated specimen of *Spiniferites* sp. (as *Hystrichosphaera* sp.) in Evitt (1967: pl. 4, fig. 14). The precingular position of the archaeopyle is further confirmed by specimens, e.g. Fig. 5 and Pl. 1, fig. 8, examined here, and for this reason *Hystrichostrogylon membraniphorum* is here transferred to *Achomosphaera* Evitt 1963. Davey & Verdier (1971: 34) maintained that *Spiniferites paradoxus* (Cookson & Eisenack) Sarjeant 1970 and *H. membraniphorum* 'were proposed to accommodate identical specimens', and that pericoel development in this group of dinoflagellate cysts does not warrant special taxonomic treatment. Specimens originally assigned to *H. membraniphorum* show no indication of sutural ridges reflecting a tabulation, and therefore they are referable to *Achomosphaera* rather than *Spiniferites*. Pericoel development in *Spiniferites* is

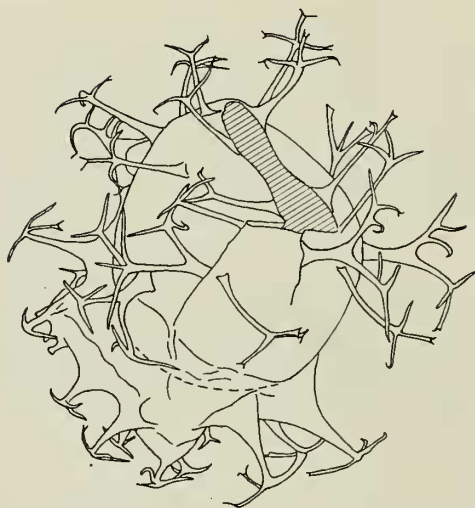


FIG. 5. *Achromosphaera membraniphora* (Agelopoulos 1964) n. comb., emend. Specimen showing the precingular archaeopyle (3'') indicated by shading, and the ventral pericoel. The broken line indicates the margin of the endophragm within the pericoel. V.57797 (3); AB40.

only known in specimens of Cretaceous age, while forms assignable to *A. membraniphora* have not been recorded from pre-Eocene sediments; the latter does seem to warrant special taxonomic treatment.

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORDS. Upper Eocene of north Germany (Agelopoulos 1964, 1967).

Genus **ADNATOSPHAERIDIUM** Williams & Downie 1966c

Adnatosphaeridium vittatum Williams & Downie 1966c

Pl. 2, fig. 1

1966c *Adnatosphaeridium vittatum* Williams & Downie: 215; pl. 24, figs 3, 7; text-fig. 56.

DIMENSIONS. Observed range: cyst body (without operculum) $35 \times 36 \mu$ to $44 \times 48 \mu$; processes, length up to 30μ , breadth up to 20μ . ($n = 10$).

REMARKS. The processes show considerable variation in breadth and are frequently very broad (up to 20μ). Distally they are united by interconnecting ribbon-like trabeculae which are particularly broad and membranous in the vicinity of the interconnections.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene of northern Spain (Caro 1973, doubtful attribution); Lower Eocene of the London Basin in southern England (Williams & Downie 1966c).

***Adnatosphaeridium multispinosum* Williams & Downie 1966c**

Pl. 2, fig. 2

1966c *Adnatosphaeridium multispinosum* Williams & Downie : 216 ; pl. 24, fig. 5 ; text-fig. 58.

DESCRIPTION. Specimens here assigned to *A. multispinosum* have numerous typically slender processes, which are simple or branched and distally united by slender trabeculae bearing numerous erect spines. The processes rarely exceed half the mean diameter of the cyst body in length, and may appear to be irregularly distributed on it, or may be organized into arcuate, soleate or annular complexes.

DIMENSIONS. Observed range : cyst body $30 \times 36 \mu$ to $46 \times 58 \mu$; length of processes up to 28μ . ($n = 22$).

REMARKS. In addition to the typical forms of *A. multispinosum*, specimens have been recorded which show a reduction in the number of trabeculae, resulting in some of the processes being distally free.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene of northern Spain (Caro 1973) ; Lower Eocene of northern Spain (Caro 1973) and of the Hampshire Basin in southern England (Williams & Downie 1966c) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

***Adnatosphaeridium robustum* (Morgenroth 1966a) n. comb.**

Pl. 2, fig. 3

1966a *Cannosphaeropsis robustum* Morgenroth : 19, pl. 4, fig. 1.

DESCRIPTION. Cyst body subspherical to ellipsoidal with a finely granular surface. Processes slender, typically simple, rarely branched, distally expanded and united by trabeculae of variable breadth. Acuminate spines occasionally present on the trabeculae. Archaeopyle apical, tetratabular.

DIMENSIONS. Observed range : diameter of cyst body $37-50 \mu$; length of processes up to 26μ . ($n = 6$).

REMARKS. Specimens recorded here exhibit an apical, tetratabular archaeopyle, and are thus attributable to *Adnatosphaeridium*. *A. robustum* is distinguished from *A. vittatum* Williams & Downie 1966c by not having broad processes, and from *A. multispinosum* Williams & Downie 1966c by having fewer processes, and only occasionally showing the development of spines on the trabeculae.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Lower Eocene of northern France (Gruas-Cavagnetto 1970b) and of north Germany (Morgenroth 1966a).

Genus *ARANEOSPHERA* nov.

DERIVATION OF NAME. Latin, *araneum*, cobweb, with reference to the form of the membrane which distally unites the processes in this genus.

DIAGNOSIS. Dinoflagellate cysts having a spherical or subspherical body with a smooth or finely fibro-reticulate surface. Processes intratabular, fibrous, simple or branched. A variable proportion of the processes are distally united by fibrous membrane. Processes invariably present on the apical, pre- and postcingular and antapical zones. Typically each reflected plate area has one process, sometimes more than one. Cingular zone usually, but not invariably, devoid of processes. Basic reflected tabulation 4', 6'', 5-6''', 0-1p, 1''''; archaeopyle precingular, formed by displacement of plate 3''.

TYPE SPECIES. *Araneosphaera araneosa* gen. et sp. nov.; Bracklesham Beds, Upper Eocene, Isle of Wight, England.

REMARKS. In the form and fibrous nature of its processes, and the position of its archaeopyle, *Araneosphaera* n. gen. is similar to *Cordosphaeridium* Eisenack 1963b emend. Morgenroth 1968, but is distinguished from the latter by having a membrane distally uniting its processes, and usually by not having processes on the cingular zone. Eisenack (1963b) probably encountered specimens attributable to *Araneosphaera* which he included in *Cordosphaeridium*, since in his original diagnosis for the latter genus, describing the processes, he says: 'At the tips the fibres diverge in paintbrush-like fashion, however may also unite together in net-like fashion' (translated from German in Norris & Sarjeant 1965:20). Morgenroth (1968: pl. 45, fig. 9) figured a specimen from the Danian, attributing it to *Cordosphaeridium inodes* (Klumpp) Eisenack 1963b emend. Morgenroth 1968, in which there is clearly membrane distally uniting the processes. Whether this should be assigned to *Araneosphaera* cannot be determined until the distribution of its processes is known. In *Araneosphaera* the distal membrane frequently shows fenestrations, but the individual areas of membrane can rarely be described as trabeculate. In having distally united processes, *Araneosphaera* shows some similarity to *Adnatosphaeridium* Williams & Downie 1966c and *Cannosphaeropsis* O. Wetzel 1933 emend. Williams & Downie 1966c. *Adnatosphaeridium* does not have fibrous processes, and the archaeopyle is apical, tetratabular. *Cannosphaeropsis* similarly does not have fibrous processes, and although the archaeopyle is precingular, this genus is distinguished by the sutural position of its processes. *Membranilarnacia* Eisenack 1963a emend. Williams & Downie 1966c has distally united processes which may be fibrous, but is distinguished from *Araneosphaera* by having an apical, tetratabular archaeopyle. In having a cingular zone which is usually, but not invariably, devoid of processes, and additional processes on the hypotract between the primary post-ingular processes and the antapical process, *Araneosphaera* shows some similarity to *Areosphaeridium* Eaton 1971a. The latter is distinguished by its apical, tetratabular archaeopyle, the distinctive form of its processes, and the absence of membrane distally uniting the processes.

***Araneosphaera araneosa* n. sp.**

Fig. 6; Pl. 2, figs 5-8

DERIVATION OF NAME. Latin, *araneosus*, full of webs, with reference to the appearance of this species.

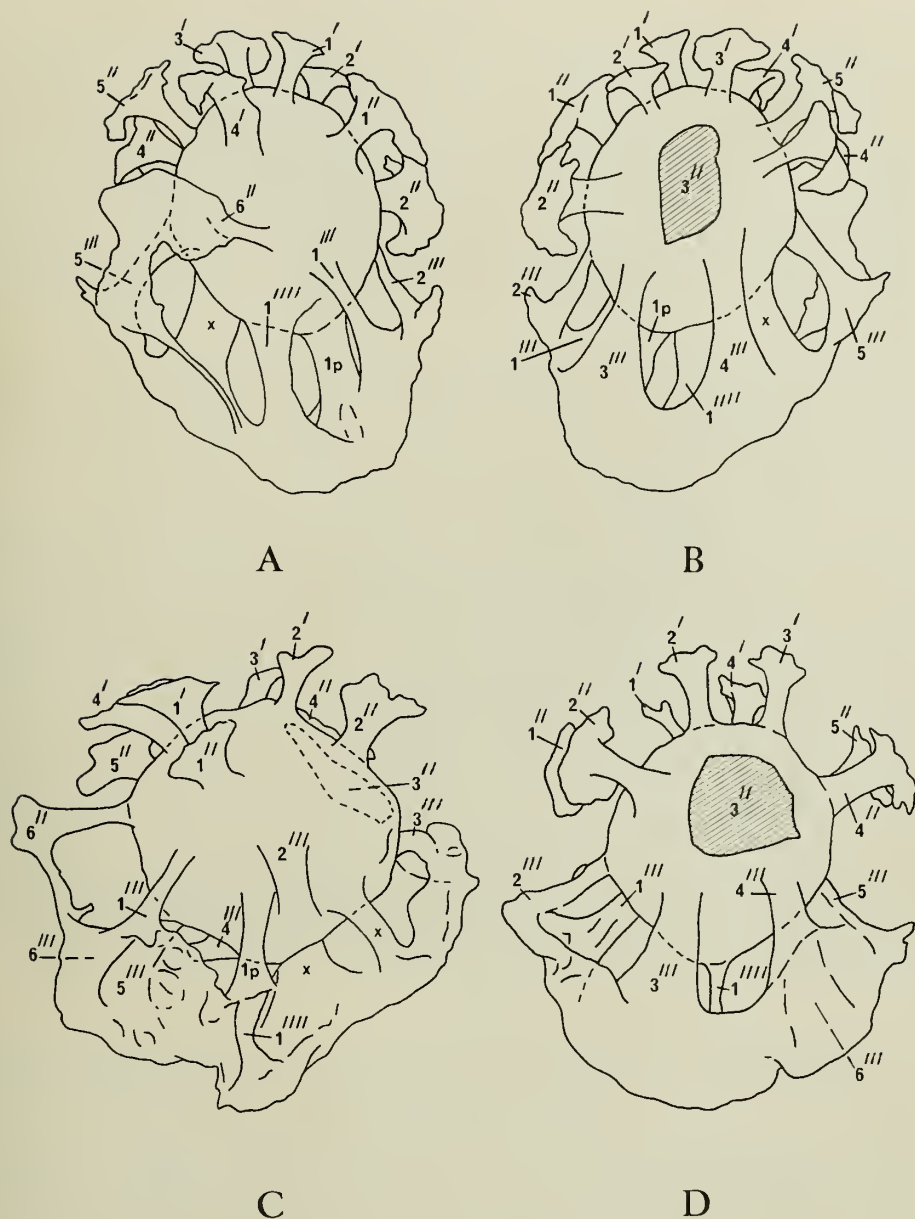


FIG. 6. *Araneosphaera araneosa* gen. et sp. nov., reflected tabulation. A, B. Holotype, ventral and dorsal views respectively. The precingular archaeopyle (3') is indicated by shading. V.57765 (2); W56. C. Ventral view; the broken line indicates the position of the archaeopyle on the dorsal surface. V.57793 (1); AB40. D. Dorsal view; the archaeopyle is indicated by shading. V.57797 (1); AB40. In A, B and C, x indicates additional processes.

DIAGNOSIS. Cyst body spherical or subspherical with a smooth or finely fibroreticulate surface. Processes intratabular, fibrous, simple or branched, proximally and distally expanded, may exhibit stem fenestration. Apical and precingular processes short, usually distally free, one per reflected plate area. Cingular zone typically devoid of processes, but an occasional one may be present. Processes on postcingular and antapical zones longer than those on the epitract, distally united by a usually irregularly fenestrate fibrous membrane. On these zones there is basically one process per reflected plate area. Additional processes are present, intermediate in position between the postcingular and antapical processes. Reflected tabulation 4', 6'', 5-6''', 0-1p, 1''''; archaeopyle precingular, formed by displacement of plate 3''.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57765 (2). Sample W56, bed 19c, Bracklesham Beds, Upper Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: overall $103 \times 82 \mu$; diameter of cyst body 50μ ; length of processes up to 38μ . Observed range: overall $94 \times 83 \mu$ to $110 \times 110 \mu$; diameter of cyst body $44-58 \mu$; length of processes up to 43μ . ($n = 20$).

REMARKS. The majority of the apical and precingular processes are typically distally free. Occasionally some of these processes may be distally united, while process 6'' is usually distally united across the cingular zone with the postcingular processes. Occasionally a process can be interpreted as being cingular in position, but the cingular zone is typically devoid of processes. The precingular and antapical processes are always distally united by fibrous membrane which frequently shows the development of irregular fenestrations. These processes are often branched, and may show stem fenestration. Up to four additional processes have been observed between, and distally united with, the five or six primary postcingular processes and the antapical process. One of these is interpreted as reflecting the posterior intercalary plate (1p), while the others possibly represent additional process development on the postcingular zone. The combination of process form and distribution, archaeopyle position, and the presence of membrane distally uniting the hypotractal processes, distinguishes *Araneosphaera araneosa* n. sp. from all described species of dinoflagellate cyst.

OCCURRENCE. Middle and Upper Eocene.

Genus **AREOLIGERA** Lejeune-Carpentier 1938 emend. Williams & Downie 1966c

The *Areoligera senonensis* complex

The genus *Areoligera* was defined by Lejeune-Carpentier (1938), *Areoligera senonensis* being the type species, with two other clearly related species, *A. coronata* and *A. medusettiformis*, distinguished essentially by the form of their processes. The description of all three species was based on specimens from the Upper Cretaceous (Senonian) of Belgium and Germany, and they are characterized by the development of process complexes on the dorsal surface of the cyst body. On the ventral surface the processes are restricted to the peripheral zone as in *Cyclonephelium* Deflandre & Cookson 1955 emend. Williams & Downie 1966c.

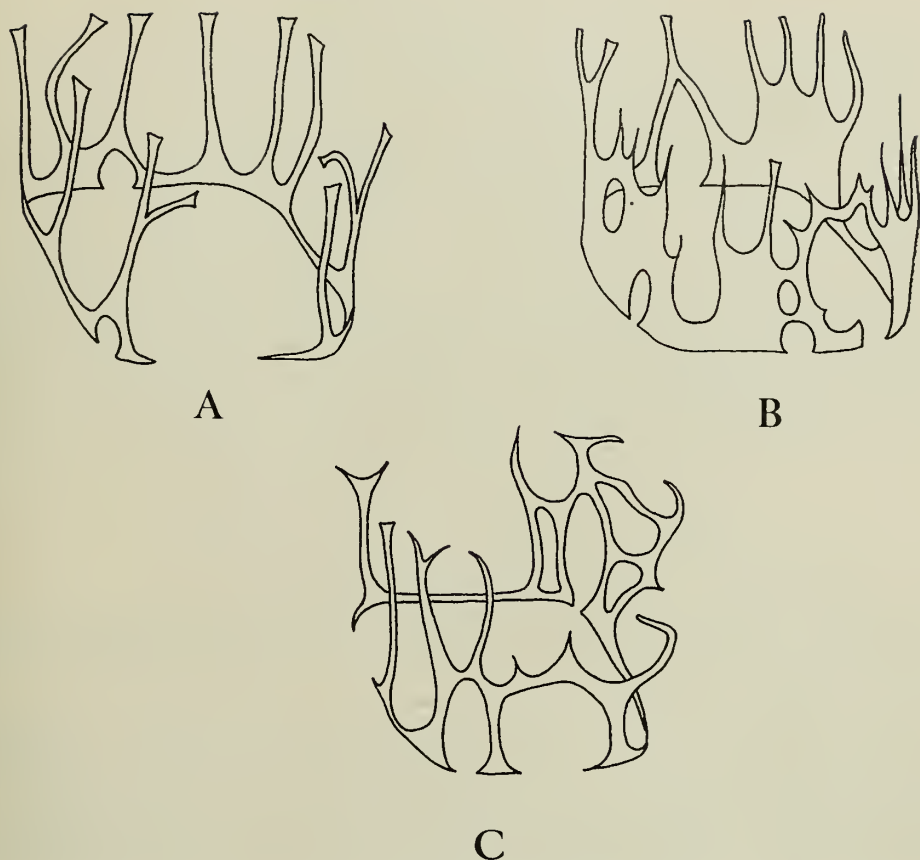


FIG. 7. Diagrammatic representation of process form in the *Areoligera senonensis* complex. A. *Areoligera senonensis* Lejeune-Carpentier 1938 and *A. cf. senonensis*. B. *Areoligera coronata* (O. Wetzel) Lejeune-Carpentier 1938 and *A. cf. coronata*. C. *Areoligera medusettiformis* (O. Wetzel) Lejeune-Carpentier 1938 and *A. cf. medusettiformis*.

Specimens assignable to *A. senonensis*, *A. coronata* and *A. medusettiformis* are here recorded in association with morphologically similar forms in which process complexes are developed on the ventral and dorsal surfaces. The latter forms were also recorded from the Lower Eocene of southern England by Williams & Downie 1966c as *A. cf. senonensis*, *A. cf. coronata* and *A. cf. medusettiformis*, with a reflected tabulation of 4', 6'', 5''', 1p, 1''''.

These six closely related taxa are here considered to represent the morphological extremes of what is informally termed the *Areoligera senonensis* complex. Three basic process types are present in the forms assigned to this complex (Fig. 7). The majority of the specimens examined exhibit more than one process type, although, apart from transitional forms, one type is dominant. The six taxa have been distinguished on the basis of the following features :

Areoligera senonensis: The majority of the processes are simple, slender, frequently distally expanded, and usually proximally united by a low membrane (Fig. 7A). Process complexes are only developed on the dorsal surface.

Areoligera cf. *senonensis*: Dominant process form as in *A. senonensis*; process complexes are developed on the ventral and dorsal surfaces.

Areoligera coronata: The majority of the processes are broad and membranous, frequently fenestrate, and have a digitate distal margin (Fig. 7B). Process complexes are only developed on the dorsal surface.

Areoligera cf. *coronata*: Dominant process form as in *A. coronata*; process complexes are developed on the ventral and dorsal surfaces.

Areoligera medusettiformis: The majority of the processes are slender, distally expanded, and as well as being typically proximally united by a low membrane, adjacent processes are united by arched trabeculae which usually bear free spines (Fig. 7C). Process complexes are only developed on the dorsal surface.

Areoligera cf. *medusettiformis*: Dominant process form as in *A. medusettiformis*; process complexes are developed on the ventral and dorsal surfaces.

***Areoligera senonensis* Lejeune-Carpentier 1938**

Pl. 3, fig. 1

1938 *Areoligera senonensis* Lejeune-Carpentier: B164, text-figs 1-3.

DIMENSIONS. Observed range: cyst body (without operculum) $36 \times 48 \mu$ to $42 \times 60 \mu$; length of processes up to 18μ . ($n = 2$).

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Senonian) of Belgium (Lejeune-Carpentier 1938); Palaeocene and Lower Eocene of the London Basin in southern England (Downie, Husain & Williams 1971); Lower Eocene of northern France (Gruas-Cavagnetto 1970b); Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

***Areoligera* cf. *senonensis* Lejeune-Carpentier 1938**

Pl. 3, figs 4-5

1966c *Areoligera* cf. *senonensis* Lejeune-Carpentier; Williams & Downie; 230; pl. 25, fig. 6; text-fig. 64.

DIMENSIONS. Observed range: cyst body (without operculum) $42 \times 56 \mu$ to $69 \times 84 \mu$; length of processes up to 20μ . ($n = 14$).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Palaeocene and Lower Eocene of north Germany (Gocht 1969, as *Areoligera senonensis*) and of the London Basin in southern England (Williams & Downie 1966c, Downie, Husain & Williams 1971*); Middle Eocene and questionably from the Middle Oligocene of north Germany (Gocht 1969, as *Areoligera senonensis*).

***Areoligera coronata* (O. Wetzel) Lejeune-Carpentier 1938**

Pl. 3, fig. 2

- 1933 *Hystrichosphaera penicillata* (Ehrenberg) O. Wetzel forma *coronata* O. Wetzel : 41 ; pl. 4, fig. 17.
 1938 *Areoligera coronata* (O. Wetzel) Lejeune-Carpentier : B170, text-fig. 6.

DIMENSIONS. Observed range : cyst body (without operculum) $40 \times 54 \mu$ to $58 \times 66 \mu$; length of processes up to 18μ . ($n = 5$).

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Senonian) of north Germany (O. Wetzel 1933) ; Upper Cretaceous (Maastrichtian) of New Jersey, U.S.A. (Evitt 1961, as *Areoligera* cf. *senonensis*), and of Denmark (Wilson 1971, as *A. senonensis* – pl. 3, fig. 9 only) ; Lower Eocene of northern Spain (Caro 1973), and of the Hampshire and London Basins in southern England (Williams & Downie 1966c) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

***Areoligera* cf. *coronata* (O. Wetzel) Lejeune-Carpentier 1938**

Pl. 3, fig. 6

- 1966c *Areoligera* cf. *coronata* (O. Wetzel) Lejeune-Carpentier ; Williams & Downie : 228 ; pl. 25, fig. 5 ; text-fig. 63.

DIMENSIONS. Observed range : cyst body (without operculum) $40 \times 45 \mu$ to $60 \times 82 \mu$; length of processes up to 26μ . ($n = 10$).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of the London Basin in southern England (Williams & Downie 1966c ; Downie, Husain & Williams 1971*).

***Areoligera medusettiformis* (O. Wetzel) Lejeune-Carpentier 1938**

Pl. 3, fig. 3

- 1933 *Hystrichosphaera penicillata* (Ehrenberg) O. Wetzel forma *medusettiformis* O. Wetzel : 41 ; pl. 4, fig. 19.
 1938 *Areoligera medusettiformis* (O. Wetzel) Lejeune-Carpentier : B170, text-figs 5, 7.

DIMENSIONS. Observed range : cyst body (without operculum) $45 \times 48 \mu$ to $60 \times 66 \mu$; length of processes up to 16μ . ($n = 5$).

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Senonian) of north Germany (O. Wetzel 1933) and of Belgium (Lejeune-Carpentier 1938) ; Cretaceous/Tertiary boundary (Maastrichtian–Danian) of Belgium (Wilson 1971, as *Areoligera senonensis* – pl. 3, fig. 8 only) ; Lower Palaeocene (Danian) of Denmark (Morgenroth 1968, as *A. coronata*) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

Areoligera cf. *medusettiformis* (O. Wetzel) Lejeune-Carpentier 1938

Pl. 3, fig. 7

1966c *Areoligera* cf. *medusettiformis* (O. Wetzel) Lejeune-Carpentier; Williams & Downie: 229; pl. 25, fig. 4.

DIMENSIONS. Observed range: cyst body (without operculum) $40 \times 42 \mu$ to $66 \times 80 \mu$; length of processes up to 30μ . ($n = 10$).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of northern Spain (Caro 1973) and of the London Basin in southern England (Williams & Downie 1966c).

Areoligera sentosa n. sp.

Fig. 8A; Pl. 4, figs 1-2; Pl. 5, figs 1, 3

DERIVATION OF NAME. Latin, *sentosus*, thorny or spiny, with reference to the spiny distal margin of the membranes.

DIAGNOSIS. Cyst body dorsoventrally flattened with a smooth or finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Ventral and dorsal surfaces bear sail-like membranes with incised distal margins which form curved troughs and pointed crests surmounted by erect or curved acuminate spines. Ventral membrane restricted to the peripheral zone, aligned parallel to, and situated close to, the margin of the cyst body. Dorsal membranes organized into process complexes which may be arcuate, soleate or annular on the pre- and postcingular zones, linear on the cingular zone, and annular on the antapical zone. Archaeopyle apical, tetratabular.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57794 (5). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body (without operculum) $61 \times 77 \mu$, height of membrane (including spines) up to 25μ . Observed range: cyst body (without operculum) $52 \times 58 \mu$ to $64 \times 80 \mu$, height of membrane (including spines) up to 32μ . ($n = 26$).

REMARKS. The sail-like membranes have a striated fibrous texture apparently due to the presence of numerous minute fenestrations; they may also show the development of large proximal fenestrations. There is some variation in the type of process complex developed on the dorsal surface. Of the three precingular and three postcingular complexes, in both zones, the middle complex is typically arcuate or soleate, while the other two are soleate or annular. Up to four linear complexes have been observed on the cingular zone; the antapical complex is annular. No forms have been recorded with process complexes developed on the ventral surface. The presence of sail-like membranes and the distinctive form of their distal margins distinguish *Areoligera sentosa* n. sp. from all described species of *Areoligera*.

OCCURRENCE. Middle and Upper Eocene.

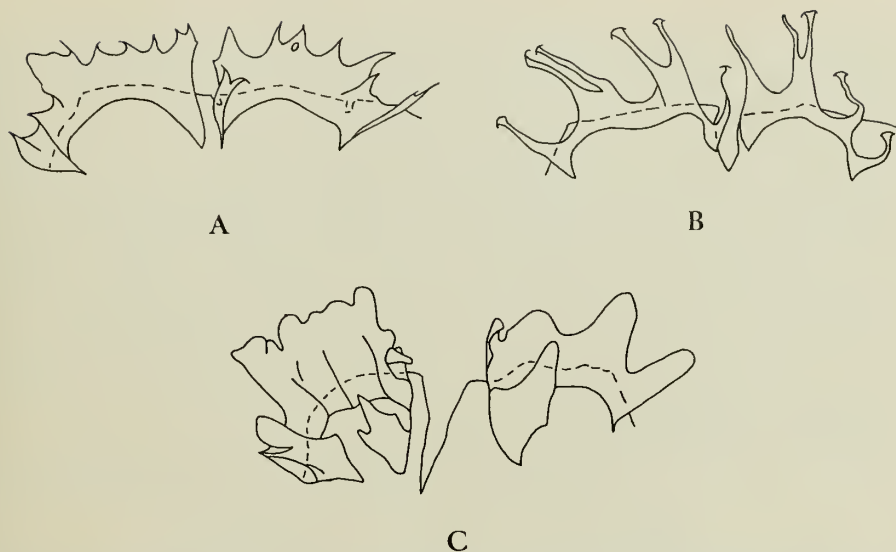


FIG. 8. Process form in three new species of *Areoligera*. A. *Areoligera sentosa* n. sp. V.57767 (2); W56. B. *Areoligera tauloma* n. sp. V.57764 (4); W56. C. *Areoligera undulata* n. sp. V.57800 (2); AB44.

***Areoligera tauloma* n. sp.**

Fig. 8B; Pl. 4, figs 3, 5; Pl. 5, figs 5–6

DERIVATION OF NAME. Greek, T, tau cross, $\lambda\omega\mu\alpha$, fringe or border, with reference to the T-shaped terminations of the spines projecting from the distal margin of the membranes.

DIAGNOSIS. Cyst body dorsoventrally flattened with a smooth or finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Ventral and dorsal surfaces bear sail-like membranes with deeply incised distal margins bearing numerous spines whose distal terminations are generally T-shaped, although a few may be blunt or acuminate. Ventral membrane restricted to the peripheral zone, aligned parallel to, and situated close to, the margin of the cyst body. Dorsal membranes organized into process complexes which may be arcuate, soleate or annular on the pre- and postcingular zones, linear on the cingular zone, and annular on the antapical zone. Archaeopyle apical, tetratabular.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57768 (3). Sample W57, bed 19c. Bracklesham Beds, Upper Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body (without operculum) $59 \times 68 \mu$; height of membrane (including spines) up to 32μ . Observed range: cyst body (without operculum) $44 \times 50 \mu$ to $62 \times 76 \mu$; height of membrane (including spines) up to 32μ . ($n = 31$).

REMARKS. The textural appearance of the membranes is similar to that of *A. sentosa* n. sp. The T-shaped distal terminations of the spines projecting from the membranes are formed by slightly recurved distal bifurcations, one part being sometimes longer than the other; blunt or acuminate terminations when present are always in a small minority. The variation in the type of process complex developed on the dorsal surface in *A. tauloma* is similar to that shown by *A. sentosa*. When linear complexes are developed on the cingular zone they are restricted to the lateral margins. No forms have been recorded with process complexes developed on the ventral surface. *A. tauloma* is distinguished from *A. sentosa* by having T-shaped terminations on the spinate distal extensions of the membranes. *Cyclonephelium ordinatum* Williams & Downie 1966c has T-shaped distal terminations on its processes, but differs from *A. tauloma* in the distribution, extent and type of process complex development and the overall appearance of its processes.

OCCURRENCE. Middle and Upper Eocene.

***Areoligera undulata* n. sp.**

Figs 8C, 9; Pl. 4, figs 4, 6; Pl. 5, figs 2, 4

1954 *Palmnickia* sp. indet. Eisenack: 70; pl. 12, fig. 20.

1961 *Palmnickia* sp. ex aff. *P. lobifera* Eisenack; Evitt: 400; pl. 8, figs 16–17; pl. 9, figs 8–10.

DERIVATION OF NAME. Latin, *undulatus*, wavy, with reference to the undulating nature of the distal margin of the membranes.

DIAGNOSIS. Cyst body dorsoventrally flattened with a smooth or finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Ventral and dorsal surfaces bear sail-like membranes with lobate undulating distal margins. Ventral membrane restricted to the peripheral zone, aligned parallel to, and situated close to, the margin of the cyst body. Dorsal membranes organized into process complexes which may be arcuate, soleate or annular on the pre- and postcingular zones, linear on the cingular zone, and annular on the antapical zone. Archaeopyle apical, tetratabular.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57802 (3). Sample AB44, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body (without operculum) $56 \times 82 \mu$; height of membrane up to 30μ . Observed range: cyst body (without operculum) $52 \times 54 \mu$ to $73 \times 92 \mu$; (complete) $66 \times 68 \mu$ to $75 \times 75 \mu$; height of membrane up to 32μ . ($n = 25$).

REMARKS. A specimen assignable to *Areoligera undulata* n. sp. was recorded from the Upper Eocene of East Prussia by Eisenack (1954), described in the text as *Palmnickia* sp. indet., and on the plate explanation as *Palmnickia* sp. ex aff. *lobifera* (Eisenack 1954: 70; pl. 12, fig. 20). Evitt (1961: 400; pl. 8, figs 16–17; pl. 9, figs 8–10) illustrated and described the specimen recorded by Eisenack, and commented on its affinities with the genus *Areoligera*, noting in particular the overall shape and the distribution of the processes.

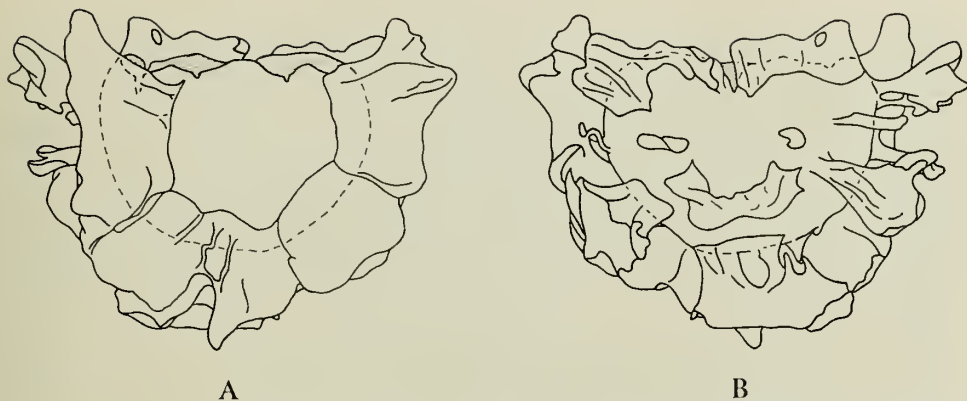


FIG. 9. *Areoligera undulata* n. sp. Holotype. A. Ventral view; the broken line indicates the margin of cyst body, the apical archaeopyle indicated by shading. B. Dorsal view. V.57802 (3); AB44.

The textural appearance of the membranes, and the variation in the type of process complex developed on the dorsal surface in *A. undulata*, are similar to those of *A. sentosa* n. sp. A few specimens have been recorded in which all the pre- and postcingular complexes are annular, while in some forms they are all arcuate. No forms have been recorded with process complexes developed on the ventral surface, although in one specimen there is some loss of proximal continuity in the membrane on the ventral surface. The undulating nature of the distal margin of the sail-like membranes and the absence of distal spines distinguish *A. undulata* from *A. sentosa* n. sp. and *A. tauloma* n. sp.

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORD. Upper Eocene of East Prussia (Eisenack 1954, as *Palmnickia* sp. indet.).

Genus *AREOSPHERIDIUM* Eaton 1971a

The genus and the three species so far assigned to it, mentioned below, have been fully described by Eaton (1971a).

Areosphaeridium diktyoplokus (Klumpp) Eaton 1971a

Pl. 6, fig. 2

1953 *Hystichosphaeridium diktyoplokus* Klumpp: 392; pl. 18, figs 3–7.

1963b *Cordosphaeridium diktyoplokus* (Klumpp) Eisenack: 262; pl. 29, fig. 1.

1971a *Areosphaeridium diktyoplokus* (Klumpp) Eaton: 358; pl. 1, figs 3–8; pl. 2, figs 1–6.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1972*), of north Germany (Morgenroth 1966a) and of the Hampshire Basin in southern England (Eaton 1971a); Middle Eocene of north Germany (Klumpp 1953, Agelopoulos

1967) and of the Hampshire Basin (Eaton 1971a); Upper Eocene of the Aleutian Islands, north Pacific Ocean (Evitt 1970*) including subsurface, offshore (Evitt 1973), of East Prussia (Eisenack 1954), of north Germany (Klumpp 1953, Agelopoulos 1967) and of the Hampshire Basin (Eaton 1971a); Eocene, undifferentiated, of Argentina (Archangelsky 1969*, Archangelsky & Fasola 1971), of Chile (Cookson & Cranwell 1967), of Romania (Balteş 1969) and of the Norwegian North Sea, subsurface, offshore (Jardine & Raynaud 1972); Middle and Upper Oligocene of north Germany (Maier 1959); ? Oligocene of Chile (Archangelsky & Fasola 1971 – indicated as possible reworking); Lower Tertiary, undifferentiated, of Antarctica (in erratics: Cranwell *et al.* 1960 as *Hystrichosphaeridium* sp., Cranwell 1964, McIntyre & Wilson 1966*, Wilson 1967a) and of Tierra del Fuego, Argentina, (Menendez 1965 as *Hystrichosphaeridium dictyostilum*, Baldis 1966); Miocene of Romania (Balteş 1967*). This species has also been recorded as a reworked form in subsurface, offshore glacial sediments of Antarctica (Wilson 1968b) and in the Pleistocene of New Zealand (Wilson 1973).

***Areosphaeridium arcuatum* Eaton 1971a**

Pl. 6, fig. 1

1971a *Areosphaeridium arcuatum* Eaton: 360; pl. 3, figs 1–9; text-figs 4–5.

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORDS. Middle and Upper Eocene of the Hampshire Basin in southern England (Eaton 1971a).

***Areosphaeridium multicornutum* Eaton 1971a**

Pl. 6, fig. 3

1971a *Areosphaeridium multicornutum* Eaton: 363; pl. 4, figs 1–7; text-fig. 6.

OCCURRENCE. Upper Eocene.

PREVIOUS RECORD. Upper Eocene of the Hampshire Basin in southern England (Eaton 1971a).

Genus ***CANNOSPHAEROPSIS*** O. Wetzel 1933 emend. Williams & Downie 1966c

***Cannosphaeropsis reticulensis* Pastiels 1948**

Pl. 2, fig. 4

1948 *Cannosphaeropsis reticulensis* Pastiels: 49; pl. 5, figs 7–10.

DIMENSIONS. Observed range: diameter of cyst body 30–39 μ ; length of processes up to 16 μ . ($n = 8$).

REMARKS. The processes in *C. reticulensis* are sutural and gonal in position, simple or proximally branched, and distally united by slender flexuous trabeculae which occasionally bear acuminate spines. When present, the archaeopyle is precingular in position.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS (not including records of this species attributed to *Adnatosphaeridium*). Palaeocene and Lower Eocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*); Lower Eocene of Belgium (Pastiels 1948, Morgenroth 1966a – doubtful attribution), of the Hampshire Basin (Williams & Downie 1966c) and of the London Basin in southern England (Williams & Downie 1966c, Gruas-Cavagnetto 1970c*); Upper Eocene of north Germany (Alberti 1961); Upper Eocene, Lower and Middle Oligocene of Northern France (Chateauneuf & Gruas-Cavagnetto 1968*).

Genus **CHIROPTERIDIUM** Gocht 1960

Chiropteridium cf. *dispersum* Gocht 1960

Fig. 10; Pl. 7, fig. 4

DESCRIPTION. Cyst body dorsoventrally flattened with a finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Sail-like membranous processes are present on the ventral and dorsal surfaces; they are arcuate in cross-section, variable in breadth, and frequently exhibit large fenestrations. The processes are finely striated and have a pseudo-fibrous appearance and their distal margins vary from entire to deeply incised. The distal terminations may be digitate, secate or acuminate. The majority of the processes are concentrated on the peripheral zone of the cyst body, where they are arranged in two rows, one on the ventral and the other on the dorsal surface. The rows are close to, and approximately parallel to, the margin of the



FIG. 10. *Chiropteridium* cf. *dispersum* Gocht 1960. Complete specimen characteristically showing the majority of the processes concentrated on the peripheral zone of the dorsoventrally flattened cyst body. V.57753 (3); W38.

cyst body. Processes are also present on the mid-ventral and mid-dorsal areas. They are sparsely distributed and show a variation in form similar to that of the processes on the peripheral zone. Archaeopyle apical, tetratabular.

DIMENSIONS. Observed range: cyst body $31 \times 37 \mu$ to $58 \times 54 \mu$; length of processes up to 26μ . ($n = 16$).

REMARKS. The specimens assigned to *C. cf. dispersum* are similar to *C. dispersum* Gocht 1960 in overall form, but differ in having fewer additional processes on the mid-dorsal and mid-ventral areas, and a smaller proportion of distally deeply incised processes on the peripheral zone.

OCCURRENCE. Lower and Middle Eocene.

Genus ***CORDOSPHAERIDIUM*** Eisenack 1963b emend. Morgenroth 1968

Cordosphaeridium inodes (Klumpp) Eisenack 1963b emend. Morgenroth 1968

Pl. 6, fig. 5

1953 *Hystrichosphaeridium inodes* Klumpp: 391; pl. 18, figs 1–2.

1963b *Cordosphaeridium inodes* (Klumpp) Eisenack: 261; pl. 29, fig. 3.

1968 *Cordosphaeridium inodes* (Klumpp) Eisenack emend. Morgenroth: 549; pl. 46, figs 1–8; not pl. 45, fig. 9.

DIMENSIONS. Observed range: diameter of cyst body 39 – 50μ ; length of processes up to 20μ . ($n = 11$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Palaeocene (Danian) of California, U.S.A. (Drugg 1967) and of Denmark (Morgenroth 1968); Palaeocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968), of northern Spain (Caro 1973 – doubtful attribution), of Tasmania (Cookson & Eisenack 1967a – doubtful attribution) and of Victoria, Australia (Cookson & Eisenack 1967b); Lower Eocene of Belgium (De Coninck 1965, 1967*, 1968, Morgenroth 1966a), of northern France (Chateauneuf & Gruas-Cavagnetto 1968, Gruas-Cavagnetto 1968, 1970b), of north Germany (Morgenroth 1966a, Gocht 1969), of northern Spain (Caro 1973 – doubtful attribution), of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*), and of Victoria, Australia (Deflandre & Cookson 1955); Middle Eocene of northern France (Gruas-Cavagnetto 1971*), of north Germany (Klumpp 1953, Agelopoulos 1967, Gocht 1969) and of the Hampshire Basin (Gruas-Cavagnetto 1970a*); Upper Eocene of Belgium (Rozen 1965), of north Germany (Klumpp 1953, Agelopoulos 1967) and of the Hampshire Basin (Gruas-Cavagnetto 1970a*); ? Upper Eocene of north Germany (Gocht 1969); Eocene, undifferentiated, of Victoria, Australia (Deflandre & Cookson 1955); Middle Oligocene of north Germany (Gerlach 1961, Gocht 1969, Benedek 1972) and of the Hampshire Basin (Gruas-Cavagnetto 1970a*); Upper Oligocene of north Germany (Gerlach 1961, Brosius 1963, Benedek 1972); Oligocene, undifferentiated, of Victoria (Cookson 1953, as *Hystrichosphaeridium truncigerum*); Middle Miocene of north Germany (Gerlach 1961).

***Cordosphaeridium exilimurum* Davey & Williams 1966b**

Pl. 6, fig. 8

1966b *Cordosphaeridium exilimurum* Davey & Williams : 87 ; pl. 11, fig. 2.

DIMENSIONS. Observed range : diameter of cyst body 45–65 μ ; processes, length up to 30 μ , breadth up to 30 μ . ($n = 8$).

REMARKS. The processes are frequently broad, and typically fenestrate. The specimens here attributed to this species indicate that the archaeopyle is precingular in position, and not apical as stated by Davey & Williams (1966b).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*).

***Cordosphaeridium fibrospinosum* Davey & Williams 1966b**

Pl. 6, fig. 6

1966b *Cordosphaeridium fibrospinosum* Davey & Williams : 86 ; pl. 5, fig. 5.

DIMENSIONS. Observed range : diameter of cyst body 40–70 μ ; processes, length up to 15 μ , breadth up to 26 μ . ($n = 6$).

REMARKS. The specimens here attributed to this species, and those recorded by Gocht (1969), indicate that the archaeopyle is precingular in position and not apical as stated by Davey & Williams (1966b).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Senonian) of Natal, South Africa (Davey 1969b) ; Palaeocene of north Germany (Gocht 1969) and of northern Spain (Caro 1973) ; Lower Eocene of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*) ; Middle Eocene of north Germany (Gocht 1969) and of northern France (Gruas-Cavagnetto 1971*) ; ? Upper Eocene of north Germany (Gocht 1969) ; Middle and Upper Oligocene of north Germany (Benedek 1972).

***Cordosphaeridium gracilis* (Eisenack) Davey & Williams 1966b**

Pl. 6, fig. 7

1954 *Hystrichosphaeridium inodes* Klumpp subsp. *gracilis* Eisenack : 66 ; pl. 8, fig. 17 ; pl. 10, figs 3–8 ; pl. 12, figs 7, 21.

1963b *Cordosphaeridium inodes* (Klumpp) Eisenack subsp. *gracilis* (Eisenack) Eisenack : 261 ; pl. 29, fig. 2.

1966b *Cordosphaeridium gracilis* (Eisenack) Davey & Williams : 84 ; pl. 3, fig. 8 ; pl. 11, figs 4, 6–7 ; text-fig. 19.

DIMENSIONS. Observed range : diameter of cyst body 53–72 μ ; length of processes up to 52 μ . ($n = 13$).

REMARKS. The slender processes are simple or branched ; when branched they are distinctly Y-shaped.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Pastiels 1948, as *Hystrichosphaeridium tubiferum* ; Morgenroth 1966a), of northern France (Gruas-Cavagnetto 1970b*), of north Germany (Morgenroth 1966a, Gocht 1969) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b ; Downie, Husain & Williams 1971) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) and of north Germany (Agelopoulos 1967, Gocht 1969) ; Upper Eocene of East Prussia (Eisenack 1938, as *Hystrichosphaera* cf. *ramosa* ; Eisenack 1954), of north Germany (Agelopoulos 1967) and of the Hampshire Basin (Gruas-Cavagnetto 1970a*) ; ? Upper Eocene of north Germany (Gocht 1969) ; Middle Oligocene of north Germany (Gerlach 1961, Gocht 1969, Benedek 1972) ; Upper Oligocene of north Germany (Benedek 1972) ; Middle Miocene of north Germany (Gerlach 1961).

***Cordosphaeridium ? minimum* (Morgenroth) Benedek 1972**

Pl. 7, figs 1-3

1966a *Cordosphaeridium inodes* Klumpp subsp. *minimum* Morgenroth : 24 ; pl. 5, figs 6-7.

1972 *Cordosphaeridium minimum* (Morgenroth) Benedek : 25 ; pl. 9, fig. 3 ; text-fig. 8.

DIMENSIONS. Observed range : diameter of cyst body 18-28 μ ; length of processes up to 12 μ . ($n = 10$).

REMARKS. This species is here questionably assigned to *Cordosphaeridium*. The thin-walled, distally expanded processes have numerous thickened ribs which extend to the distal margin ; their overall appearance is not comparable to the typical fibrous appearance of the processes in *Cordosphaeridium*. The process ribs usually extend onto the surface of the cyst body where they intersect to form a complex system of polygonal fields. The position of the archaeopyle is uncertain, but the specimens here recorded show some indication that it may possibly be apical in position. Morgenroth (1966a) recorded one specimen showing an elliptical opening, while Benedek (1972) did not observe any significant openings.

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of north Germany (Morgenroth 1966a) ; Middle Oligocene of north Germany (Benedek 1972).

***Cordosphaeridium multispinosum* Davey & Williams 1966b**

Pl. 6, fig. 4

1966b *Cordosphaeridium multispinosum* Davey & Williams : 89 ; pl. 3, fig. 6.

DIMENSIONS. Observed range : diameter of cyst body 42-60 μ ; length of processes up to 18 μ . ($n = 10$).

REMARKS. The numerous short fibrous processes in *C. multispinosum* have a delicate appearance, are simple or branched, occasionally proximally united, and usually slightly expanded distally.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1972*), of northern France (Gruas-Cavagnetto 1968, Chateauneuf & Gruas-Cavagnetto 1968*) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b); Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

Genus **CYCLONEPHELIUM** Deflandre & Cookson 1955
emend. Williams & Downie 1966c

Cyclonephelium divaricatum Williams & Downie 1966c

Pl. 7, fig. 5

1966c *Cyclonephelium divaricatum* Williams & Downie : 223 ; pl. 25, fig. 1 ; text-fig. 60.

DIMENSIONS. Observed range : cyst body (without operculum) $42 \times 48 \mu$ to $66 \times 68 \mu$; length of processes up to 21μ . ($n = 11$).

REMARKS. Characterized by the presence of distal spines and secæ arising from the trabeculae or perforated membranes which complexly unite the processes.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of the Hampshire and London Basins in southern England (Williams & Downie 1966c, Downie, Husain & Williams 1971*) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

Cyclonephelium exuberans Deflandre & Cookson 1955

Pl. 8, figs 1-2

1948 *Membranilarnax pterospermoides* O. Wetzel ; Pastiels : 46 ; pl. 5, figs 11, 13-14 ; not fig. 12.

1955 *Cyclonephelium exuberans* Deflandre & Cookson : 285 (nom. nud.).

1966c *Cyclonephelium exuberans* Deflandre & Cookson ; Williams & Downie : 225 (in part) ; not text-fig. 61.

1973 *Cyclonephelium pastielsi* Deflandre & Cookson ; Caro : 352 (in part) ; pl. 1, fig. 8.

DIAGNOSIS. Cyst body dorsoventrally flattened with a smooth or finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Processes restricted to the peripheral zone of the cyst body ; variable in breadth and simple or branched, distally complexly united by trabeculae and areas of variably fenestrate membrane. No processes developed on reflected precingular plates 3'' and 6''. Archaeopyle apical, tetratabular.

HOLOTYPE. The specimen figured as *Membranilarnax pterospermoides* O. Wetzel 1933 by Pastiels (1948 : pl. 5, figs 11, 13) ; Lower Eocene, Quenast, Belgium.

DIMENSIONS. Holotype : cyst body (without operculum) $29 \times 39 \mu$; length of processes up to 25μ . Observed range (this study) : cyst body $54 \times 50 \mu$ to $80 \times 80 \mu$; length of processes up to 38μ . ($n = 26$).

REMARKS. Deflandre & Cookson (1955 : 285) applied the name *Cyclonephelium exuberans* as a new species to forms described from the Lower Eocene of Belgium by Pastiels (1948) as *Membranilarnax pterospermoides* O. Wetzel 1933. However, no holotype was designated, thus rendering the species invalid under Art. 37 of the I.C.B.N. To rectify this point one of the specimens illustrated by Pastiels (1948 : pl. 5, figs 11, 13) is here designated as holotype, and a diagnosis given. Pastiels provided four illustrations of *M. pterospermoides* (Pastiels 1948 : pl. 5, figs 11–14). The concept of *C. exuberans* is here restricted to forms similar to the specimen represented by a photograph in Pastiels (1948 : pl. 5, fig. 11), and a probable camera lucida drawing (pl. 5, fig. 13). A diagrammatic representation of the same specimen, which is devoid of processes on reflected precingular plates 3'' and 6'', is given in pl. 5, fig. 14. Other specimens, similar to that illustrated by Pastiels (1948 : pl. 5, fig. 12) with processes developed on all the precingular plates, are here assigned to *C. aff. exuberans*.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene and Lower Eocene of northern Spain (Caro 1973, as *C. pastielsi* in part) ; Lower Eocene of Belgium (Pastiels 1948, as *M. pterospermoides*, pl. 5, figs 11, 13–14 only ; De Coninck 1967*, 1972*) and of the Hampshire and London Basins in southern England (Williams & Downie 1966c, in part, not text-fig. 61 ; Downie, Husain & Williams 1971*).

Cyclonephelium aff. *exuberans* Deflandre & Cookson 1955 *ex* Eaton 1976

Pl. 7, fig. 7

- 1948 *Membranilarnax pterospermoides* O. Wetzel ; Pastiels : 46 ; pl. 15, fig. 12 ; not figs 11, 13–14.
- 1966c *Cyclonephelium exuberans* Deflandre & Cookson ; Williams & Downie : 225 (in part) ; text-fig. 61.
- 1966c *Cyclonephelium pastielsi* Deflandre & Cookson ; Williams & Downie : 227 ; pl. 25, fig. 2.
- 1969 *Cyclonephelium pastielsi* Deflandre & Cookson ; Gocht : 60 ; pl. 8, fig. 15.
- 1971 *Cyclonephelium pastielsi* Deflandre & Cookson ; Downie, Husain & Williams : pl. 1, fig. 12.
- 1972 *Cyclonephelium exuberans* Deflandre & Cookson ; Benedek : 8 ; pl. 1, fig. 5.
- 1973 *Cyclonephelium pastielsi* Deflandre & Cookson ; Caro : 352 (in part) ; not pl. 1, fig. 8.

DIMENSIONS. Observed range : cyst body $54 \times 54 \mu$ to $75 \times 80 \mu$; length of processes up to 40μ . ($n = 5$).

REMARKS. In the shape and surface ornamentation of the cyst body, the form of the processes and the complex development of distal trabeculae and variably fenestrate membrane, *C. aff. exuberans* is very similar to *C. exuberans*, but is distinguished in usually having processes developed on all six reflected precingular

plates. The processes on reflected plates 3'' and 6'' may be reduced in size, and in some specimens one of these two plates (but never both) may be devoid of processes. Although the forms here described as *C. exuberans* and *C. aff. exuberans* were originally considered to represent one species (Pastiels' concept of *M. pterospermoides* O. Wetzel 1933), the separation of the two was found to be of palynostratigraphical significance.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Palaeocene and Lower Eocene of northern Spain (Caro 1973, as *C. pastielsi* in part; not pl. 1, fig. 8); Lower Eocene of Belgium (Pastiels 1948, as *M. pterospermoides*, pl. 5, fig. 12 only; De Coninck 1965, questionably as *C. exuberans*; Morgenroth 1966a, questionably as *C. pastielsi*), of north Germany (Gocht 1969, as *C. pastielsi*) and of the Hampshire and London Basins in southern England (Williams & Downie 1966c, as *C. exuberans* in part and *C. pastielsi*; Downie, Husain & Williams 1971, as *C. pastielsi*); Middle and Upper Oligocene of north Germany (Benedek 1972, as *C. exuberans*).

Cyclonephelium intricatum Eaton 1971a

Pl. 8, fig. 6

1971a *Cyclonephelium intricatum* Eaton: 365; pl. 4, figs 8–10.

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORDS. Middle and Upper Eocene of the Hampshire Basin (Eaton 1971a); Upper Oligocene of north Germany (Brosius 1963, questionably as *C. reticulosum*).

Cyclonephelium laciniiforme Gerlach 1961

Fig. 11; Pl. 7, fig. 6

1961 *Cyclonephelium laciniiforme* Gerlach: 206; pl. 29, fig. 4.

DESCRIPTION. Cyst body dorsoventrally flattened with a subcircular outline, and a smooth or finely granular surface. Processes restricted to the peripheral zone of the cyst body, membranous and roughly T-shaped in overall form. Distally the processes are expanded, the majority united by membranous trabeculae of variable width. Archaeopyle apical, tetratabular.

DIMENSIONS. Observed range: cyst body (without operculum) $42 \times 42 \mu$ to $58 \times 66 \mu$; length of processes up to 30μ . ($n = 10$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Middle Oligocene of north Germany (Gerlach 1961; Benedek 1972, doubtful attribution); Upper Oligocene of north Germany (Brosius 1963; Benedek 1972, doubtful attribution); ? Upper Oligocene of north Germany (Gerlach 1961).



FIG. 11. *Cyclonephelium laciniiforme* Gerlach 1961. The apical archaeopyle is indicated by shading. V.57756 (8) ; W40.

***Cyclonephelium ordinatum* Williams & Downie 1966c**

Pl. 7, fig. 8

1966c *Cyclonephelium ordinatum* Williams & Downie : 225 ; pl. 25, fig. 3 ; text-fig. 62.

DIMENSIONS. Observed range : cyst body $50 \times 52 \mu$ to $68 \times 75 \mu$; length of processes up to 30μ . ($n = 9$).

REMARKS. The processes are similar to those of several members of the *Areoligera senonensis* complex (*A. coronata*, *A. cf. coronata*, *A. medusettiformis* and *A. cf. medusettiformis*). It also resembles *Areoligera* in having its processes organized into process complexes ; however, only linear and occasionally arcuate complexes are developed, and the processes are restricted to the peripheral zone of the cyst body.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Palaeocene of northern Spain (Caro 1973) ; Lower Eocene of north Germany (Gocht 1969), of northern Spain (Caro 1973) and of the Hampshire and London Basins in southern England (Williams & Downie 1966c, Downie, Husain & Williams 1971*) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) and north Germany (Gocht 1969) ; Middle Oligocene of north Germany (Benedek 1972, doubtful attribution).

***Cyclonephelium pastielsi* Deflandre & Cookson 1955**

1948 *Membranilarnax cf. livadisoides* O. Wetzel ; Pastiels : 47 ; pl. 5, fig. 15.
1955 *Cyclonephelium pastielsi* Deflandre & Cookson : 285 (nom. nud.).

- 1965 *Cyclonephelium pastielsi* Deflandre & Cookson ; De Coninck : 44 ; pl. 12, figs 32, 35, 39.
 1968 *Cyclonephelium pastielsi* Deflandre & Cookson ; Gruas-Cavagnetto : 83 ; pl. 12, fig. 4 ;
 pl. 16, fig. 14.
 1968 *Cyclonephelium pastielsi* Deflandre & Cookson ; De Coninck : 41 ; pl. 12, figs 10-11,
 15-16.
 1970 *Cyclonephelium pastielsi* Deflandre & Cookson ; Gruas-Cavagnetto : pl. 2, fig. 4.

DIAGNOSIS. See description of *Membranilarnax* cf. *liradiscoides* O. Wetzel 1933 by Pastiels (1948 : 47).

HOLOTYPE. The specimen figured as *Membranilarnax* cf. *liradiscoides* O. Wetzel 1933 by Pastiels (1948 : pl. 5, fig. 15) ; Lower Eocene, Quenast, Belgium.

DIMENSIONS. Holotype : cyst body (without operculum) $53 \times 57 \mu$; length of processes up to 30μ .

REMARKS. As in the case of *Cyclonephelium exuberans*, Deflandre & Cookson (1955 : 285) also failed to designate a holotype for *Cyclonephelium pastielsi*, their new species name for forms described from the Lower Eocene of Belgium by Pastiels (1948) as *Membranilarnax* cf. *liradiscoides* O. Wetzel 1933. However, since he only provided one illustration of *M.* cf. *liradiscoides* (Pastiels 1948 : pl. 5, fig. 15, a probable camera lucida drawing) this must be the holotype, and it is here designated as such. Pastiels' original description of this form (1948 : 47) indicates that it consists of a central body with processes restricted to the peripheral zone. The processes are simple or bifurcate, distally ramified and interconnected, and the illustrated specimen is devoid of them on reflected precingular plates 3'' and 6''. In overall form the specimen illustrated by Pastiels is more closely comparable to *Cyclonephelium retiintertextum* Cookson 1965 (De Coninck 1968 : 41) than *C. exuberans* (Williams & Downie 1966c : 225, 227). On this basis, *C. pastielsi* can only be considered to have been recorded from the Lower Eocene of Belgium (Pastiels 1948, as *M.* cf. *liradiscoides* ; De Coninck 1965, 1968, Gruas-Cavagnetto 1968) and of northern France (Gruas-Cavagnetto 1968, 1970b). There are also several listed records without illustration or description which cannot be commented on : Lower Eocene of Belgium (De Coninck 1967), of northern France (Chateauneuf & Gruas-Cavagnetto 1968) and of the Hampshire Basin in southern England (Gruas-Cavagnetto 1970a) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971).

Cyclonephelium spinetum n. sp.

Fig. 12 ; Pl. 8, fig. 3

DERIVATION OF NAME. Latin, *spinetum*, thorn-hedge, with reference to the appearance of the spine-bearing distal trabeculae.

DIAGNOSIS. Cyst body dorsoventrally flattened with a smooth or finely granular surface. The circular or subcircular outline may be modified by the development of an antapical protuberance. Processes, restricted to the peripheral zone of the cyst body, broad and membranous, and distally expanded and united by membranous, arched trabeculae of variable width which bear numerous acuminate spines. Archaeopyle apical, tetratabular.

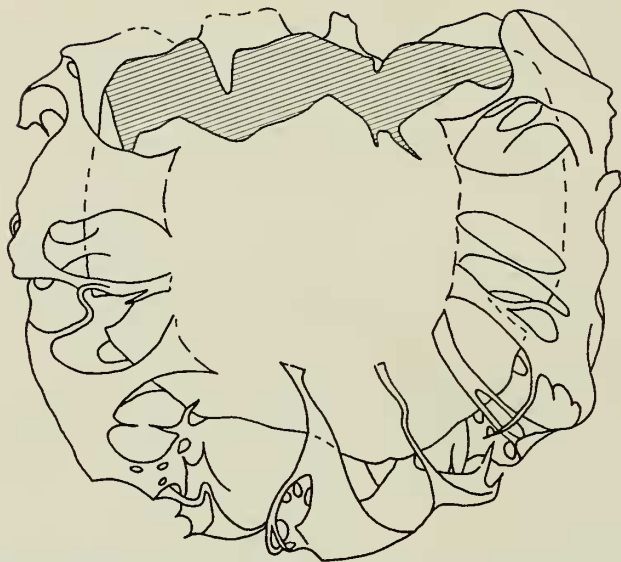


FIG. 12. *Cyclonephelium spinetum* n. sp. Holotype; the apical archaeopyle is indicated by shading. V.57742; W26A.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57742. Sample W26A, bed 9a, Bracklesham Beds, Lower Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body (without operculum) $55 \times 65 \mu$; length of processes up to 22μ . Observed range: cyst body (without operculum) $40 \times 55 \mu$ to $58 \times 68 \mu$; length of processes up to 36μ . ($n = 10$).

REMARKS. The membranous processes are smooth or finely striated. They show considerable variation in breadth, varying from very broad and proximally closely spaced to narrow and proximally widely spaced. The overall form of the processes is broadly T-shaped. The acuminate spines projecting from the distal trabeculae show considerable variation in length, while the trabeculae themselves vary from broad and ribbon-like to slender strands. *Cyclonephelium spinetum* n. sp. is similar to *C. laciniiforme* Gerlach 1961 in overall form, but differs in having numerous acuminate spines projecting from the distal trabeculae. Acuminate spines are also developed in *C. divaricatum* Williams & Downie 1966c, but this species does not have the broad membranous processes which are typical of *C. spinetum*.

OCCURRENCE. Lower and Middle Eocene.

Cyclonephelium vicinum n. sp.

Fig. 13; Pl. 8, figs 4-5

DERIVATION OF NAME. Latin, *vicinus*, near or neighbouring, with reference to the periphragm which remains close to the endophragm where the two layers are separated.

DIAGNOSIS. Cyst body dorsoventrally flattened with a circular or subcircular outline. The finely granular periphragm is separated from, but remains close to, the endophragm over the peripheral zone of the cyst body. The separated periphragm is wrinkled and folded. Fenestrations may be developed adjacent to, or sometimes away from, the line of separation. Archaeopyle apical, tetratabular.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57744. Sample W26A, bed 9a, Bracklesham Beds, Lower Eocene, Whitecliff Bay, Isle of Wight, England.

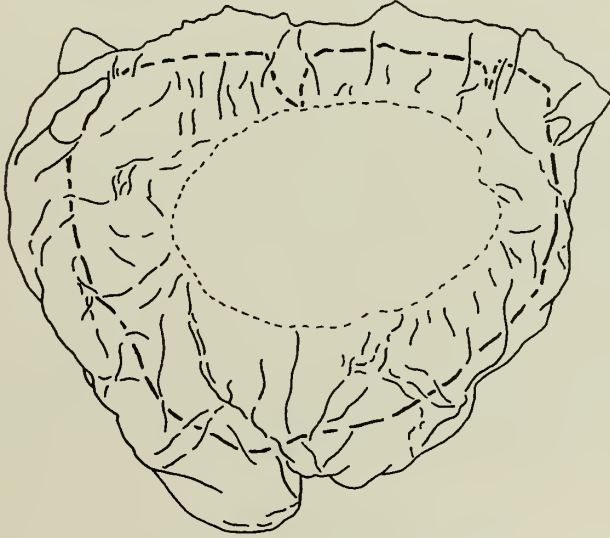


FIG. 13. *Cyclonephelium vicinum* n. sp. Holotype, showing the characteristic wrinkling and folding in the periphragm where it is separated from the endophragm. V.57744; W26A.

DIMENSIONS. Holotype: cyst body (without operculum) $54 \times 67 \mu$; height of pericoel up to 14μ . Observed range: cyst body (without operculum) $45 \times 50 \mu$ to $68 \times 77 \mu$; height of pericoel up to 18μ . ($n = 18$).

REMARKS. The development of several fenestrations in the separated periphragm adjacent to the line of separation may give the appearance of a row of distally united membranous processes. The presence of a marginal pericoel distinguishes *C. vicinum* n. sp. from all described species of *Cyclonephelium*. In overall form the specimens here described are similar to those recorded from the Middle Oligocene of north Germany by Gocht (1969) as *Chiropteridium aspinatum* (Gerlach) Brosius 1963, but in *C. vicinum* the separated periphragm usually lies closer to the endophragm. The assignment of Gocht's specimens to *Chiropteridium* seems questionable, and it is possible that *C. vicinum* may be an evolutionary predecessor of the forms described by Gocht. This problem cannot be resolved until forms of intermediate age have been studied.

OCCURRENCE. Lower, Middle and Upper Eocene.

Genus *DIPHYES* Cookson 1965 emend. Davey & Williams 1966b

Diphyes colligerum (Deflandre & Cookson) Cookson 1965
emend. Davey & Williams 1966b

Pl. 8, fig. 7

1955 *Hystrichosphaeridium colligerum* Deflandre & Cookson : 178 ; pl. 7, fig. 3.

1965 *Diphyes colligerum* (Deflandre & Cookson) Cookson : 86 ; pl. 9, figs 1-12.

1966b *Diphyes colligerum* (Deflandre & Cookson) Cookson emend. Davey & Williams : 96 ;
pl. 4, figs 2-3.

DIMENSIONS. Observed range : diameter of cyst body 24-40 μ ; length of slender processes up to 20 μ ; length of antapical process up to 20 μ . (n = 15).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Questionably from the Upper Cretaceous, probable Senonian, of Victoria, Australia (Cookson 1965) ; Palaeocene of South Dakota, U.S.A. (Stanley 1965), of Tasmania (Cookson & Eisenack 1967a), of Victoria (Cookson & Eisenack 1967b) and of France (Chateauneuf & Gruas-Cavagnetto 1968) ; Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1968), of northern France (Gruas-Cavagnetto 1968, 1970b*, Chateauneuf & Gruas-Cavagnetto 1968), of north Germany (Morgenroth 1966a), of the Hampshire and London Basins in southern England (Davey & Williams 1966b) and of Victoria (Deflandre & Cookson 1955) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) ; Upper Eocene of Belgium (Rozen 1965), of Victoria (Cookson 1965) and of the Aleutian Islands, north Pacific Ocean (Evitt 1970*) ; Eocene, undifferentiated, of Western Australia (Cookson & Eisenack 1961) ; ? Oligocene of Victoria (Cookson 1953, as *Hystrichosphaeridium* sp. c).

Genus *DISTATODINIUM* nov.

DERIVATION OF NAME. Latin, *distatus*, differed, stood apart, with reference to the distinctive form of the processes.

DIAGNOSIS. Dinoflagellate cysts in which the cyst body has an oval or elongate oval outline. Processes simple or branched, variable in breadth, flattened and blade-like in cross-section, proximally expanded and frequently united by a membrane, distally expanded and ramified. Ramifications typically, but not invariably, complex. Occasionally, slender tubular processes are present. The number of processes varies from about 14 (in some specimens without an operculum) to about 60 or more. Processes aligned into rows parallel to the long axis of the cyst body, and apparently situated on or close to reflected plate boundaries ; many are also arranged in a more or less circular manner around the cyst body. Archaeopyle apical.

TYPE SPECIES. *Distatodinium craterum* gen. et sp. nov., Bracklesham Beds, Upper Eocene, Isle of Wight, England.

REMARKS. Three features suggest that the processes in *Distatodinium* gen. nov. are basically sutural in position, their distribution pattern over the cyst body, the occasional presence of processes which are T-shaped in cross-section and probably

gonal in position and the occurrence of proximal membrane uniting processes across reflected tabulation zone boundaries. However, in some specimens of *D. ellipticum* (Cookson 1965) n. comb., processes are present which cannot be interpreted as sutural, and some are arranged in arcuate complexes. The reflected tabulation of *Distatodinium* has not been determined, but process distribution in *D. craterum* n. sp. suggests there are six precingular and at least five postcingular plates. The majority of the flattened blade-like processes appear to be solid, particularly in the proximal region. This is emphasized by a straight or curved line at the base of the processes, marking their divergence from the cyst body. There is some indication that the distal ramifications may be hollow, and some very slender tubular processes have been observed. Two described genera, *Prolixosphaeridium* Davey *et al.* 1966b and *Tanyosphaeridium* Davey & Williams 1966b, are comparable to *Distatodinium* in having an elongate cyst body and an apical archeopyle. In *Prolixosphaeridium* the distribution of the processes may be similar to *Distatodinium*, but they are distally less complex, being not obviously blade-like in cross-section or proximally united by membrane. In *Tanyosphaeridium* the processes are again distally less complex, and they are considered to be intratabular in distribution. They are also cylindrical, and circular or subcircular in cross-section.

In addition to the species assigned to *Distatodinium* and described in this paper, one other species is also transferred to the genus. This is *Distatodinium tenerum* (Benedek 1972) n. comb. = *Tanyosphaeridium tenerum* Benedek 1972 : 35 ; pl. 10, figs 13-14 ; text-fig. 14. Middle Oligocene, north Germany.

Distatodinium craterum n. sp.

Pl. 9, figs 1-5

1961 *Hystriochosphaeridea* Scherer : fig. 2.

DERIVATION OF NAME. Greek *κράτερός*, strong, with reference to the appearance of the broad processes.

DIAGNOSIS. The cyst body has an elongate oval outline and a smooth or finely granular surface. The processes are typically broad, simple or branched, flattened and blade-like in cross-section, distally and proximally expanded. Distally they are bifurcate or trifurcate with complex secondary and tertiary branchlets, the ramifications having a twig-like appearance. Typically 13 to 17 processes on specimens which have lost the operculum ; there are six processes on the precingular and five on the postcingular zone. Cingular zone devoid of processes. Usually one, sometimes two processes at the antapical pole. Between one and four additional processes may be present, apparently intermediate in position between the primary postcingular and antapical processes. The processes are also arranged into six rows parallel to the long axis of the cyst body. The straight or curved lines marking the divergence of the processes from the cyst body are also parallel to the long axis. Adjacent longitudinally aligned processes may be proximally united by membrane. Archaeopyle apical.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57792. Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body (without operculum) $44 \times 30 \mu$; processes, length up to 22μ , breadth up to 7μ . Observed range: cyst body (without operculum) $35 \times 20 \mu$ to $55 \times 38 \mu$; processes, length up to 30μ , maximum breadth $5-11 \mu$. ($n = 25$).

REMARKS. No detached or in place opercula have been observed in *D. craterum* n. sp. The observed maximum number of processes is 17, but in the majority of specimens there are 14. The flattening and alignment of the processes parallel to the long axis of the cyst body, and the development of membrane proximally uniting longitudinally aligned processes in separate reflected tabulation zones, strongly suggest that the processes are sutural in position. This would indicate the presence of six precingular plates and at least five postcingular plates. *D. craterum* is distinguished from all described species here attributed to *Distatodinium* by the overall broader and stronger form of its processes. It is further distinguished from *D. ellipticum* (Cookson 1965) n. comb. by having considerably fewer processes (about 14 as opposed to about 40 or more in *D. ellipticum*), and from *D. tenerum* (Benedek 1972) n. comb. by again having considerably fewer processes which are longer, and distally more complex.

OCCURRENCE. Upper Eocene.

PREVIOUS RECORD. Middle Oligocene of Switzerland (Scherer 1961, as *Hystriosphæridea*).

***Distatodinium ellipticum* (Cookson 1965) n. comb.**

Pl. 9, figs 7-9

1965 *Hystriosphæridium ellipticum* Cookson : 87; pl. 11, figs 1-3, 3a.

1969 *Tanyosphaeridium ellipticum* (Cookson) Davey & Williams : 7.

1972 *Tanyosphaeridium ellipticum* (Cookson) Davey & Williams; Benedek : 35; pl. 9, figs 13-14; pl. 10, fig. 2.

DESCRIPTION. The cyst body has an elongate oval outline and a smooth or finely granular surface. The processes are variable in breadth, simple or branched, typically flattened and blade-like in cross-section, and distally and proximally expanded. Distally they are bifurcate or trifurcate with complex secondary and tertiary branchlets, the ramifications having a twig-like appearance. The number of processes varies from about 40 to about 60. They appear to be present over all zones of the cyst body, but frequently show a greater concentration towards the apex and antapex. The processes show some alignment into rings around the cyst body, and a definite alignment into rows parallel to its long axis. The straight or curved lines marking the divergence of the processes from the cyst body are also parallel to the long axis. Occasionally processes occur which are T-shaped in cross-section. Adjacent longitudinally aligned processes may be proximally united by membrane, particularly at the antapex. Archaeopyle apical.

DIMENSIONS. Observed range: cyst body (without operculum) $40 \times 25 \mu$ to $73 \times 48 \mu$; processes, length up to 30μ , breadth up to 7μ . ($n = 24$).

REMARKS. The flattened processes appear to be essentially solid, particularly in the proximal region. Occasionally the distal ramifications may be hollow (Cookson 1965 : 87 ; pl. 11, fig. 3a), and some specimens of *D. ellipticum* have been recorded here with a few very slender tubular processes. The flattening and alignment of the processes parallel to the long axis of the cyst body in *D. ellipticum* may indicate that the processes are basically sutural in position, and the occasional process which is T-shaped in cross-section is probably gonial in position. However, the processes cannot be attributed to reflected tabulation zones as readily as in *D. craterum* n. sp., and their occasional arrangement in arcuate complexes complicates the interpretation of process distribution in *D. ellipticum*.

OCCURRENCE. Upper Eocene.

PREVIOUS RECORDS. Upper Eocene of Victoria, Australia (Cookson 1965) ; Middle and Upper Oligocene of north Germany (Benedek 1972).

***Distatodinium paradoxum* (Brosius 1963) n. comb.**

Pl. 9, fig. 6

- 1963 *Hystrichosphaeridium paradoxum* Brosius : 41 ; pl. 4, figs 1, 6 ; text-fig. 2 (nos 1a-c).
 1969 *Tanyosphaeridium paradoxum* (Brosius) Gocht : 54 ; pl. 7, figs 5-8 ; text-fig. 39.
 1969 ? *Oligosphaeridium paradoxum* (Brosius) Davey & Williams : 5.
 1972 *Tanyosphaeridium paradoxum* (Brosius) Gocht ; Benedek : 35 ; pl. 9, fig. 12 ; pl. 10, fig. 6.

DESCRIPTION. The cyst body has an oval or elongate oval outline and a smooth or finely granular surface. The processes are typically slender, simple or branched, distally and proximally expanded, usually flattened and blade-like in cross-section, occasionally tubular. Distally they are bifurcate or trifurcate with some secondary and tertiary branchlets at the extremities. The number of processes is about 20 and their distribution is similar to that of *D. craterum* n. sp. In addition to the alignment of the processes into rings around the cyst body, there is also some alignment into rows parallel to the long axis of the cyst body. The straight or curved lines marking the divergence of the processes from the cyst body are also usually parallel to the long axis. Adjacent longitudinally aligned processes may be proximally united by membrane. Archaeopyle apical. One specimen (Pl. 9, fig. 6) shows partial detachment of the polar region. If this is interpreted as the apical zone, the operculum bears four processes, two of which are proximally united by membrane.

DIMENSIONS. Observed range : cyst body, length (with operculum) $46\ \mu$, length (without operculum) $36-52\ \mu$, breadth $28-42\ \mu$; length of processes up to $24\ \mu$. (n = 6).

REMARKS. As has been suggested for *D. craterum* n. sp., the processes in *D. paradoxum* are possibly sutural in position. On this basis, and assuming the polar breakage represents archaeopyle formation, the illustrated specimen can be interpreted as having four apical plates, six precingular plates, and at least five post-cingular plates.

OCCURRENCE. Upper Eocene.

PREVIOUS RECORDS. Middle Oligocene of north Germany (Gocht 1969, Benedek 1972); Upper Oligocene of north Germany (Brosius 1963, Benedek 1972).

Genus **EOCLADOPYXIS** Morgenroth 1966a

Eocladopyxis peniculatum Morgenroth 1966a

Pl. 8, fig. 8

1966a *Eocladopyxis peniculatum* Morgenroth : 7; pl. 3, figs 2-3.

DIMENSIONS. Observed range: diameter of cyst body $28-50\ \mu$; length of processes up to $11\ \mu$. ($n = 12$).

REMARKS. The majority of the specimens here recorded show partial separation of the plate areas. The figured specimen shows the loss of the apical zone in archaeopyle formation, and the separation of the plates on the dorsal surface, particularly the narrow, elongate cingular plates.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORD. Lower Eocene of north Germany (Morgenroth 1966a).

Genus **GONYAULACYSTA** Deflandre *ex* Norris & Sarjeant 1965,
emend. Sarjeant 1969

Gonyaulacysta tenuitabulata (Gerlach) De Coninck 1968

Fig. 14; Pl. 8, fig. 9

1961 *Gonyaulax tenuitabulata* Gerlach : 159; pl. 25, figs 10-11; text-figs 1-3.

1968 *Gonyaulacysta tenuitabulata* (Gerlach) De Coninck : 23; pl. 5, figs 9-10, 13-16.

DIMENSIONS. Observed range: overall $48 \times 42\ \mu$ to $88 \times 84\ \mu$; length of apical horn up to $8\ \mu$. ($n = 14$).

REMARKS. *G. tenuitabulata* has a delicate appearance, and the plate boundaries are marked by low, simple thickenings of the periphragm, defining a tabulation of 4', 6'', 6c, 6''', 1p, 1p.v., 1''''.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1968); Middle Oligocene and Middle Miocene of north Germany (Gerlach 1961).

Genus **HOMOTRYBLIUM** Davey & Williams 1966b

Homotryblium tenuispinosum Davey & Williams 1966b

Pl. 10, fig. 1

1966b *Homotryblium tenuispinosum* Davey & Williams : 101; pl. 4, fig. 11; pl. 12, figs 1, 5, 7; text-fig. 21.

DIMENSIONS. Observed range: cyst body $32 \times 30\ \mu$ to $60 \times 48\ \mu$; length of processes up to $38\ \mu$. ($n = 8$).

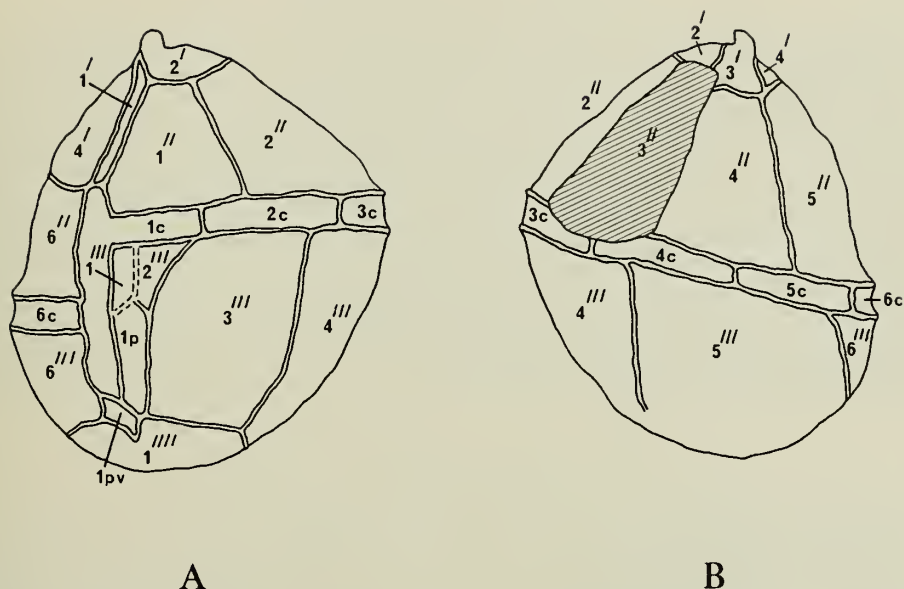


FIG. 14. *Gonyaulacysta tenuitabulata* (Gerlach) De Coninck 1968, reflected tabulation. A. Ventral view. B. Dorsal view, the precingular archaeopyle (3'') indicated by shading. V.57770 (2); W58.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of northern Spain (Caro 1973) and of the London Basin in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*).

Homotryblium abbreviatum n. sp.

Pl. 10, figs 2-4

1968 *Hystriosphæridium tubiferum brevispinum* Davey & Williams; De Coninck: 37; pl. 9, figs 24-25.

DERIVATION OF NAME. Latin, *abbreviatus*, shortened, with reference to the short processes.

DIAGNOSIS. Cyst body subspherical or spherical with a granular surface. Processes short, tubular and distally expanded; distal margin denticulate, secate or aculeate. Length of processes not exceeding one-third of the mean diameter of the cyst body. Processes intratabular, one per reflected plate area. Reflected tabulation of the form 3-4', 6'', 6c, 5-6''', 0-1p, 1''''; archaeopyle epittractal.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57782 (1). Sample AB11, bed 2g, Bracklesham Beds, Lower Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: diameter of cyst body $48\ \mu$; processes, length up to $12\ \mu$, breadth up to $8\ \mu$. Observed range: diameter of cyst body $34\text{--}48\ \mu$; processes up to $14\ \mu$, breadth up to $10\ \mu$. ($n = 11$).

REMARKS. The short processes may be slender or broad, and they are circular to subquadrate in section. The processes may show a proximal circle where they diverge from the cyst body. Up to five very slender processes have been observed on the sulcal zone. *H. abbreviatum* n. sp. differs from all described species of *Homotryblum* in having very short processes, the length of which does not exceed one-third of the mean diameter of the cyst body.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORD. Lower Eocene of Belgium (De Coninck 1968, as *Hystriosphæridium tubiferum brevispinum*).

***Homotryblum oceanicum* n. sp.**

Pl. 10, figs 5–8

DERIVATION OF NAME. Latin, *oceanus*, the sea, ocean.

DIAGNOSIS. Cyst body subspherical or spherical with a granular surface. Processes long, broad and cylindrical, and individually relatively constant in breadth, showing little distal expansion. Distal margin denticulate, secate or aculeate. Processes intratabular, one per reflected plate area. Reflected tabulation of the form 3', 6'', 6c, 5''', 1''''; archaeopyle epittractal.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57794 (1). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: diameter of cyst body $49\ \mu$; processes, length up to $28\ \mu$, breadth up to $10\ \mu$. Observed range: diameter of cyst body $36\text{--}50\ \mu$; processes, length up to $30\ \mu$, breadth up to $16\ \mu$. ($n = 12$).

REMARKS. The majority of the studied specimens are incomplete; no sulcal processes have been observed. In some specimens there is a proximal circle where the processes diverge from the cyst body. The distinctive long broad cylindrical processes, individually relatively constant in breadth, distinguish *H. oceanicum* from all described species of *Homotryblum*.

OCCURRENCE. Middle and Upper Eocene.

Genus ***HYSTRICHOKOLPOMA*** Klumpp 1953 emend. Williams & Downie 1966a

***Hystrihokolpoma eisenacki* Williams & Downie 1966a**

Pl. 10, fig. 9

1966a *Hystrihokolpoma eisenacki* Williams & Downie: 176; pl. 17, figs 1–3; text-fig. 46.

DIMENSIONS. Observed range: diameter of cyst body $36\text{--}50\ \mu$; large processes, length up to $28\ \mu$, breadth up to $28\ \mu$; antapical process, length up to $42\ \mu$, breadth up to $20\ \mu$; length of slender processes up to $20\ \mu$. ($n = 8$).

REMARKS. Williams & Downie (1966a) described *H. eisenacki* typically as having small tubules branching off from the large processes. In addition to the typical form of *H. eisenacki* recorded in this study, some specimens have been observed with both acuminate spines and tubules developed on the large processes.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1972*), of northern France (Gruas-Cavagnetto 1970b*), of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Williams & Downie 1966a); Middle and ? Upper Eocene of north Germany (Gocht 1969); Upper Eocene of East Prussia (Eisenack 1954, as *Hystrichokolpoma cinctum*); Eocene, undifferentiated, of Romania (Balteş 1969, doubtful attribution); Middle Oligocene of north Germany (Gocht 1969).

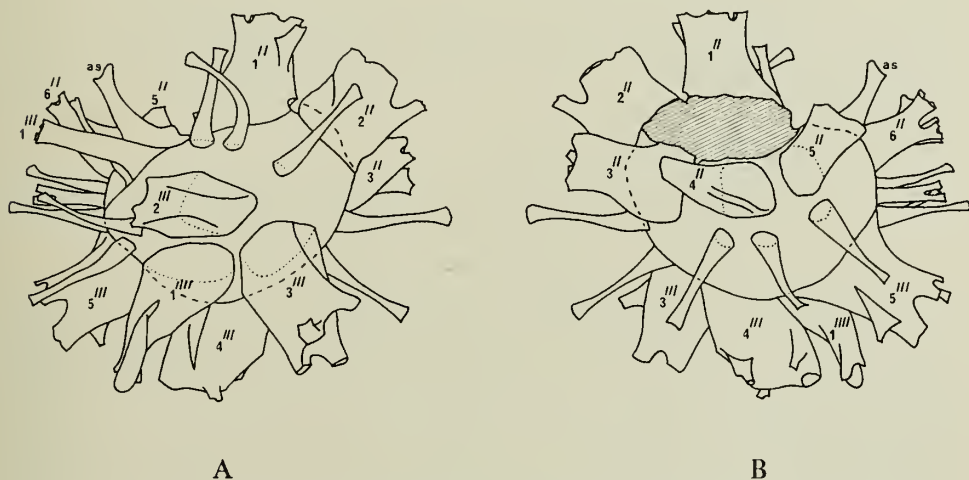


FIG. 15. *Hystrichokolpoma granulata* n. sp. Reflected tabulation of holotype. A. Ventral view. B. Dorsal view, the apical archaeopyle indicated by shading. V.57781 (6); AB11.

Hystrichokolpoma granulata n. sp.

Fig. 15; Pl. 10, figs 11–13

DERIVATION OF NAME. Latin, *granulum*, small grain, granule, with reference to the surface ornament.

DIAGNOSIS. Cyst body subspherical with a granular surface. There are two types of granular intratabular processes. Large broad cylindrical processes, restricted to the pre- and postcingular and antapical zones, split distally into short open branches, and may exhibit distal tubules. Slender open processes, restricted to the cingular and sulcal zones, are distally expanded, simple or distally branched. Reflected tabulation 4', 6'', 6c, 5''', 1''''; archaeopyle apical, tetratabular.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57781 (6). Sample AB11, bed 2g, Bracklesham Beds, Lower Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body (without operculum) $39 \times 49 \mu$; large processes, length up to 20μ , breadth up to 19μ ; antapical process, length 24μ , breadth 16μ ; length of slender processes up to 24μ . Observed range: diameter of cyst body (without operculum) $28-46 \mu$; large processes, length up to 20μ , breadth up to 19μ ; antapical process, length up to 24μ , breadth up to 16μ ; length of slender processes up to 24μ . ($n = 10$).

REMARKS. Unlike other species of *Hystrichokolpoma*, the individual plate areas are not clearly defined on the cyst body in *H. granulata* n. sp. On the circular zone there are typically two, sometimes one process per plate. The antapical process is distinctive, tapering distally with tubules typically developed close to the distal margin. The anterior sulcal process (a.s.) is larger than the other sulcal processes. The form of the apical processes has not been determined. *H. granulata* is distinguished from other species of *Hystrichokolpoma* by its distinctive granular ornament, the overall form of the processes and the lack of well-defined plate areas on the cyst body.

OCCURRENCE. Lower and Middle Eocene.

Hystrichokolpoma rigaudae Deflandre & Cookson 1955

Pl. 10, fig. 10

1955 *Hystrichokolpoma rigaudae* Deflandre & Cookson: 279; pl. 6, figs 6, 10; text-fig. 42.

DIMENSIONS. Observed range: diameter of cyst body $32-42 \mu$; large processes, length up to 26μ , breadth up to 9μ ; antapical process, length up to 26μ , breadth up to 10μ ; length of slender processes up to 20μ . ($n = 10$).

REMARKS. The large processes in *H. rigaudae* are characterized by considerable distal expansion and the development of distal tubules.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene of Victoria, Australia (Cookson & Eisenack 1967b); Lower Eocene of Belgium (De Coninck 1965, 1967*, 1972*, Morgenroth 1966a), of northern France (Gruas-Cavagnetto 1968, 1970b), of north Germany (Morgenroth 1966a), of the Hampshire Basin (Williams & Downie 1966a) and of the London Basin in southern England (Williams & Downie 1966a, Graus-Cavagnetto 1970c*) and of Victoria (Deflandre & Cookson 1955); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); ? Middle Eocene of Victoria (Deflandre & Cookson 1955); Upper Eocene of Victoria (Cookson & Eisenack 1965); Eocene, undifferentiated, of Victoria (Deflandre & Cookson 1955); Middle Oligocene of north Germany (Gerlach 1961, Benedek 1972); Upper Oligocene of north Germany (Gerlach 1961, Brosius 1963, Benedek 1972); Middle Miocene of north Germany (Maier 1959, Gerlach 1961); Miocene-Pliocene of Italy (Habib 1971*); Pleistocene of Israel (Rossignol 1962, 1964); Cenozoic, undifferentiated, of the eastern seaboard, U.S.A. (subsurface, offshore, Habib 1972).

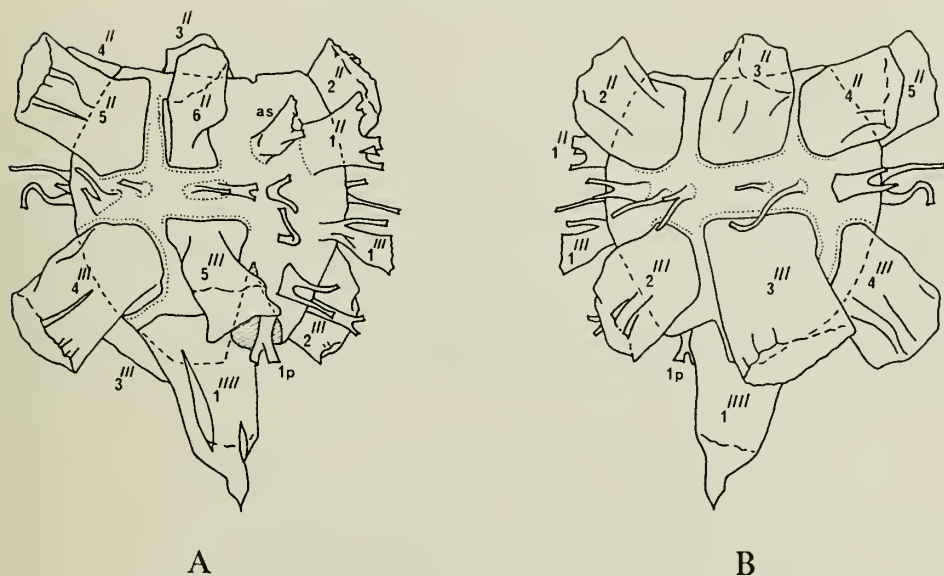


FIG. 16. *Hystrichokolpoma salacia* n. sp. Reflected tabulation of holotype. A. Ventral view. B. Dorsal view. V.57757 (6); W40.

***Hystrichokolpoma salacia* n. sp.**

Fig. 16; Pl. 11, figs 1-3

DERIVATION OF NAME. Latin, *Salacia*, goddess of the sea.

DIAGNOSIS. Cyst body subspherical with a smooth or finely granular surface. There are two types of intratabular processes. Large cylindrical processes, restricted to the pre- and postcingular and antapical zones, are subcircular or subquadrate in cross-section, distally closed, and the majority devoid of distal tubules. Processes 1'' and 1''' are reduced, may be branched and exhibit distal tubules. The slender processes, restricted to the cingular and sulcal zones, are simple or branched, and distally expanded and open. All processes have a finely striated surface. Reflected tabulation 4', 6'', 6c, 5''', 1p, 1''''; archaeopyle apical, tetratabular.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57757 (6). Sample W40, bed 11, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body (without operculum) $46 \times 44 \mu$; large processes, length up to 23μ , breadth up to 16μ ; antapical process, length 26μ , breadth 14μ ; length of slender processes up to 10μ . Observed range: diameter of cyst body (without operculum) $30-50 \mu$; large processes, length up to 24μ , breadth up to 18μ ; antapical process, length up to 36μ , breadth up to 18μ ; length of slender processes up to 16μ . (n = 20).

REMARKS. The large closed cylindrical processes are devoid of distal tubules, but they frequently show longitudinal folds. The slender processes on the cingular

zone are variable in form and number; in most specimens there are two processes per cingular plate. The antapical process is considerably longer than the other large processes and differs in overall form; it gradually tapers distally for about half to two-thirds of its length and then sharply to a restricted distal termination. The anterior sulcal process (a.s.) is larger than the other sulcal processes. The form of the apical processes has not been determined. The comparative simplicity of its large processes distinguishes *H. salacia* n. sp. from the majority of the described species of *Hystrichokolpoma*. *H. poculum* Maier 1959 also has simple large processes, but they were described by Maier (1959) as being cup-shaped and distally open.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORD. Possibly from the Eocene, undifferentiated, of Romania (Balteş 1969, as *Hystrichokolpoma eisenacki*).

Genus **HYSTRICHOSPHAERIDIUM** Deflandre 1937
emend. Davey & Williams 1966b

Hystrichosphaeridium tubiferum (Ehrenberg) Deflandre 1937
emend. Davey & Williams 1966b

Pl. 11, fig. 4

1838 *Xanthidium tubiferum* Ehrenberg: pl. 1, fig. 16.

1937 *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre: 68.

1966b *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre emend. Davey & Williams: 56; pl. 6, figs 1-2; pl. 8, fig. 5; pl. 10, fig. 2; text-fig. 13.

DIMENSIONS. Observed range: cyst body $30 \times 35 \mu$ to $48 \times 45 \mu$; length of processes 12-30 μ . (n = 6).

REMARKS. The specimens here attributed to *H. tubiferum* are similar to those recorded from the London Clay (Lower Eocene) of southern England by Davey & Williams (1966b). They exhibit slender tubular processes which show considerable distal expansion and a foliate distal margin. Occasionally some processes show the development of distal fenestration. Several records of *H. tubiferum* from the Lower Eocene and all illustrated records from younger Palaeogene and Neogene sediments in north-west Europe are probably referable to *Homotryblum* Davey & Williams 1966b; the illustrated specimens exhibit either an epitrectal archeopyle or the required process number and distribution for this genus, or both. These records are as follows: Lower Eocene of Belgium (De Coninck 1965: 25; pl. 6, figs 1-3, 6-7) and of Belgium and north Germany (Morgenroth 1966a: 31; pl. 8, figs 7-8); Upper Eocene of north Germany (Agelopoulos 1967: 37; pl. 11, fig. 2); Middle and Upper Oligocene of north Germany (Benedek 1972: 30; pl. 9, fig. 5); Upper Oligocene of north Germany (Brosius 1963: 38; pl. 8, fig. 4); Middle and Upper Oligocene and Middle Miocene of north Germany (Gerlach 1961: 184; pl. 28, fig. 2). Gruas-Cavagnetto (1970a) recorded *H. tubiferum* in large numbers from the Upper Eocene of the Hampshire Basin in southern England. The material is not illustrated, but examination of equivalent horizons in this area indicates that the

species occurring in large numbers is *Homotryblium tenuispinosum* Davey & Williams 1966b.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Cretaceous, Albian and younger – see Davey & Verdier (1971); Lower Palaeocene (Danian) of California, U.S.A. (Drugg 1967); Palaeocene to Lower Eocene of New Zealand (Wilson 1968*); Lower Eocene of Belgium (De Coninck 1967*, 1968, 1972*, Gruas-Cavagnetto 1968), of northern France (Gruas-Cavagnetto 1970b) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); Eocene, undifferentiated, of Argentina (Archangelsky 1969, doubtful attribution); Lower Tertiary, undifferentiated, of Antarctica, in erratics (McIntyre & Wilson 1966*, Wilson 1967a) and of Tierra del Fuego, Argentina (Baldis 1966); ? Tertiary of Victoria, Australia (Cookson 1953, doubtful attribution); Pleistocene of Israel (Rossignol 1964, presumably as re-working).

Hystrichosphaeridium asterium n. sp.

Pl. 11, figs 7–10

1972 *Hystrichosphaeridium pseudorecurvatum* Morgenroth; Benedek: 29; pl. 9, fig. 10.

DERIVATION OF NAME. Greek ἀστέρειος, starry, with reference to the distinctive distal termination of the processes.

DIAGNOSIS. Cyst body has a subcircular or rounded polygonal outline and a smooth surface. Processes about 20, tubular and usually slender and fairly constant in breadth. Each process is surmounted by a wide distal platform with usually 10 to 15 marginal aculei. Archaeopyle apical.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57772 (3). Sample W58, bed 19c, Bracklesham Beds, Upper Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body (without operculum) $27 \times 32 \mu$; length of processes up to 13μ . Observed range: cyst body (without operculum) $22 \times 22 \mu$ to $30 \times 34 \mu$; length of processes up to 20μ . ($n = 4$).

REMARKS. None of the observed specimens is complete. The number of processes (about 20) indicates that there is one process per plate, reflecting the tabulation of the genus. The processes are occasionally expanded proximally – in one specimen (Pl. 11, fig. 9) one process shows considerable proximal expansion. The distal platforms which surmount each process are typically recurved, sometimes flat or slightly concave. Some processes show a reduction of the distal platform; these are similar to those of *H. pseudorecurvatum* Morgenroth 1966a. Apart from the occasional presence of such processes, the small size of *H. asterium* and the distinctive form of the distal portion of its processes distinguish this species from all other described species of *Hystrichosphaeridium*.

OCCURRENCE. Upper Eocene.

PREVIOUS RECORD. Middle Oligocene of north Germany (Benedek 1972, as *H. pseudorecurvatum*).

***Hystrichosphaeridium patulum* Davey & Williams 1966b**

Pl. 11, fig. 5

1966b *Hystrichosphaeridium patulum* Davey & Williams : 60 ; pl. 10, fig. 5.

DIMENSIONS. Observed range : diameter of cyst body 12–20 μ ; length of processes 4–8 μ . ($n = 7$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1968) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b).

***Hystrichosphaeridium pseudorecurvatum* Morgenroth 1966a**

Pl. 11, fig. 6

1966a *Hystrichosphaeridium pseudorecurvatum* Morgenroth : 30 ; pl. 8, figs 5–6.

DIMENSIONS. Observed range : diameter of cyst body 21–33 μ ; length of processes 8–20 μ . ($n = 10$).

REMARKS. Morgenroth (1966a) noted up to 35 processes in some specimens of *H. pseudorecurvatum*, indicating that there may be more than one process on some plates. A variation in process number was also noted in this study, some specimens having up to 60 processes.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Morgenroth 1966a, Gruas-Cavagnetto 1968, De Coninck 1968), of northern France (Gruas-Cavagnetto 1970b*), of north Germany (Morgenroth 1966a) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b, as *H. sheppeyense*) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) ; Upper Eocene of Belgium (Rozen 1965, as *H. recurvatum*).

Genus ***LANTERNOSPHAERIDIUM*** Morgenroth 1966a

***Lanternosphaeridium lanosum* Morgenroth 1966a**

Pl. 12, fig. 1

1966a *Lanternosphaeridium lanosum* Morgenroth : 38 ; pl. 10, figs 10–11.

DIMENSIONS. Observed range : cyst body 60 $\times$ 44 μ to 68 $\times$ 50 μ ; height of membrane up to 22 μ ; length of apical horn up to 20 μ . ($n = 2$).

REMARKS. A strong simple horn is frequently developed at the apical pole. The dense fibrous membrane present over the cyst body does not show any organization into discrete processes.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium and north Germany (Morgenroth 1966a).

***Lanternosphaeridium axiale* (Eisenack) Morgenroth 1966a**

Pl. 12, fig. 2

1965 *Cordosphaeridium axiale* Eisenack : 150 ; pl. 15, figs 1-4.

1966a *Lanternosphaeridium axialis* (Eisenack) Morgenroth : 38 ; pl. 6, figs 4-5.

1969 *Lanternosphaeridium axiale* (Eisenack) Morgenroth ; Gocht : 48 ; pl. 2, figs 7-8 ; text-fig. 34.

DIMENSIONS. Observed range : cyst body $48 \times 42 \mu$ to $81 \times 63 \mu$; length of processes up to 19μ ; length of apical horn up to 21μ . ($n = 8$).

REMARKS. The numerous slender, fibrous, intratabular processes are distally expanded, usually simple, but sometimes branched.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Morgenroth 1966a) and of north Germany (Morgenroth 1966a, Gocht 1969) ; Middle Eocene of north Germany (Gocht 1969) ; Upper Eocene of north Germany (Eisenack 1965) ; ? Upper Eocene of north Germany (Gocht 1969) ; Middle Oligocene of north Germany (Gocht 1969).

***Lanternosphaeridium radiatum* Morgenroth 1966a**

Pl. 12, fig. 3

1966a *Lanternosphaeridium radiatum* Morgenroth : 37 ; pl. 10, figs 7-9.

DIMENSIONS. Observed range : cyst body $52 \times 40 \mu$ to $81 \times 69 \mu$; length of processes up to 24μ ; length of apical horn up to 48μ . ($n = 17$).

REMARKS. The numerous fibrous intratabular processes are simple or branched, variable in breadth, frequently distally expanded, and usually proximally united by fibrous membrane.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium and north Germany (Morgenroth 1966a).

***Lanternosphaeridium vectense* n. sp.**

Pl. 12, figs 4-6

DERIVATION OF NAME. From *Vectis*, the Roman name for the Isle of Wight, the type locality for this species.

DIAGNOSIS. Cyst body subspherical, longer than broad, with a strongly fibro-reticulate surface. Usually between 50 and 60 fibrous, intratabular processes which are strong, variable in breadth, and simple or branched. They are proximally

and distally expanded, and their length is less than half the mean diameter of the cyst body. The distal margins are ragged or aculeate. Apical horn strong and laterally expanded into usually three short branches. Archaeopyle precingular, formed by displacement of plate 3''.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57797 (2). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body $95 \times 83 \mu$; length of processes up to 31μ ; length of apical horn 24μ . Observed range: cyst body $66 \times 55 \mu$ to $95 \times 83 \mu$; length of processes up to 31μ ; length of apical horn up to 24μ . ($n = 18$).

REMARKS. The apical horn is typically shorter than the longest processes. The processes show considerable variation in breadth, very slender ones frequently reflecting the sulcal zone. *L. vectense* n. sp. is distinguished from *L. axiale* (Eisenack) Morgenroth 1966a by usually having a larger cyst body with a strongly fibroreticulate surface and stronger, frequently broader processes, and from *L. radiatum* Morgenroth 1966a by having stronger discrete processes which are not proximally united by fibrous membrane.

OCCURRENCE. Middle and Upper Eocene.

Genus **LEPTODINIUM** Klement 1960, emend. Wall 1967, emend. Sarjeant 1969

Leptodinium membranigerum Gerlach 1961

Pl. 8, fig. 11

1961 *Leptodinium membranigerum* Gerlach: 162; pl. 26, figs 1-4, 7; text-figs 4-5.

DIMENSIONS. Observed range: cyst body $48 \times 46 \mu$ to $66 \times 68 \mu$; height of crests up to 8μ . ($n = 7$).

REMARKS. The cyst body has a finely punctate or finely granular surface. The sutural crests are unornamented or finely granular with a smooth or slightly serrated distal margin. A very low apical prominence is sometimes developed by separation of the periphragm and endophragm.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Upper Oligocene and ? Middle Miocene of north Germany (Gerlach 1961).

Genus **LINGULODINIUM** Wall 1967

Lingulodinium machaerophorum (Deflandre & Cookson) Wall 1967

Pl. 8, fig. 10

1955 *Hystrichosphaeridium machaerophorum* Deflandre & Cookson: 274; pl. 9, figs 4, 8.

1967 *Lingulodinium machaerophorum* (Deflandre & Cookson) Wall: 109; pl. 15, figs 16-17; text-fig. 6.

DIMENSIONS. Observed range: diameter of cyst body $39-54 \mu$; length of processes up to 22μ . ($n = 8$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Palaeocene (Danian) of California (Drugg 1967, doubtful attribution); Lower Eocene of Belgium (De Coninck 1968), of northern France (Gruas-Cavagnetto 1968) and of north Germany (Morgenroth 1966a); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); Upper Eocene of the Hampshire Basin in southern England (Gruas-Cavagnetto 1970a*); Middle Oligocene of north Germany (Gerlach 1961, Benedek 1972); Upper Oligocene of north Germany (Brosius 1963, Benedek 1972); ? Upper Oligocene of north Germany (Gerlach 1961); Middle Miocene of north Germany (Maier 1959, Gerlach 1961) and of Victoria, Australia (Deflandre & Cookson 1955); Miocene-Pliocene of Italy (Habib 1971); Pleistocene of the Caribbean Sea (Wall 1967), of Israel (Rossignol 1962, as *Hystrichosphaeridium ashdodense*; 1964) and of Norfolk, England (sub-surface, Wall & Dale 1968b*). *L. machaerophorum* has also been recorded from Recent sediments, e.g. Wall & Dale (1967).

Genus *LITOSPHAERIDIUM* Davey & Williams 1966b

Litosphaeridium ? *inversibuccinum* Davey & Williams 1966b

Pl. 13, figs 1-5

1966b ? *Litosphaeridium inversibuccinum* Davey & Williams: 82; pl. 12, fig. 3.

DESCRIPTION. The forms here assigned to *L.* ? *inversibuccinum* invariably exhibit a polygonal apical archaeopyle, and 12 or 14 processes arranged in two rings which are presumed to reflect the pre- and postcingular zones. No processes have been observed at the antapex. Distally the processes are tubular with an expanded denticulate or aculeate margin; proximally they are hollow and considerably expanded, and laterally adjacent processes merge into each other. Six or eight processes have been recorded on the precingular zone, and six on the postcingular zone. The generic assignment of this species remains uncertain.

DIMENSIONS. Observed range: diameter of cyst body 12-18 μ ; length of processes up to 12 μ . ($n = 5$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1968) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*).

Genus *MEMBRANILARNACIA* Eisenack 1963a emend. Williams & Downie 1966c

Membranilarnacia ursulae (Morgenroth) De Coninck 1968

Pl. 12, fig. 7

1966a *Cannosphaeropsis ursulae* Morgenroth: 20; pl. 3, figs 11-12.

1966c *Membranilarnacia reticulata* Williams & Downie: 220; pl. 24, figs 4, 6; text-fig. 59.

1967 *Membranilarnacia diktyophora* Agelopoulos: 49; pl. 12, figs 3-4, 6.

1968 *Membranilarnacia ursulae* (Morgenroth) De Coninck: 43; pl. 13, figs 4-6.

DIMENSIONS. Observed range: diameter of cyst body $36-53\ \mu$; length of processes up to $32\ \mu$. ($n = 3$).

REMARKS. Williams & Downie (1966c) recognized two variants of this distinctive species (described as *M. reticulata* Williams & Downie 1966c) in the London Clay (Lower Eocene) of southern England. One has processes on the cingular zone, the other is devoid of processes on this zone, the latter being the more common variant. The specimens here attributed to *M. ursulae* are referable to the more common of the two variants.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1968, 1972*), of north Germany (Morgenroth 1966a), of the Hampshire Basin (Williams & Downie 1966c, as *M. reticulata*; Downie, Husain & Williams 1971*, Eaton 1971a) and the London Basin in southern England (Williams & Downie 1966c, as *M. reticulata*; Downie, Husain & Williams 1971*); Middle Eocene of north Germany (Gocht 1969) and of the Hampshire Basin (Eaton 1971a); Upper Eocene of north Germany (O. Wetzel 1935, as *Membranilarnax* sp. indet.; Eisenack 1954, as *Membranilarnax* sp. indet.; Agelopoulos 1967, as *Membranilarnacia diktyophora*).

Genus *OPERCULODINIUM* Wall 1967

Operculodinium centrocarpum (Deflandre & Cookson) Wall 1967

Pl. 15, figs 1-2

1955 *Hystrichosphaeridium centrocarpum* Deflandre & Cookson: 272; pl. 8, figs 3-4.

1967 *Operculodinium centrocarpum* (Deflandre & Cookson) Wall: 111; pl. 16, figs 1-2, 5.

DIMENSIONS. Observed range: diameter of cyst body $28-75\ \mu$; length of processes up to $31\ \mu$. ($n = 22$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Senonian) of Natal, South Africa (Davey 1969a); Lower Palaeocene (Danian) of California, U.S.A. (Drugg 1967); Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1968, Gruas-Cavagnetto 1968) and of north Germany (Morgenroth 1966a); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); Middle and Upper Eocene of the Hampshire Basin in southern England (Gruas-Cavagnetto 1970a*); Upper Eocene of north Germany (Agelopoulos 1967, doubtful attribution); Middle Oligocene of north Germany (Maier 1959, Gerlach 1961); Upper Oligocene of north Germany (Maier 1959, Gerlach 1961, Brosius 1963); Oligocene, undifferentiated, of Victoria, Australia (Cookson 1953, as *Hystrichosphaeridium* sp. b); Middle Miocene of north Germany (Maier 1959, Gerlach 1961) and of Victoria (Cookson, 1953, as *Hystrichosphaeridium* sp. a; Deflandre & Cookson 1955); Upper Miocene of north Germany (Maier 1959); Miocene-Pliocene of Italy (Habib 1971); Pleistocene of the Caribbean Sea (Wall 1967) and of Norfolk, England (subsurface, Wall & Dale 1968b); Cenozoic, undifferentiated, of the eastern seaboard, U.S.A. (subsurface, offshore, Habib 1972). *O. centrocarpum* has also been recorded from Recent sediments, e.g. Wall & Dale (1967).

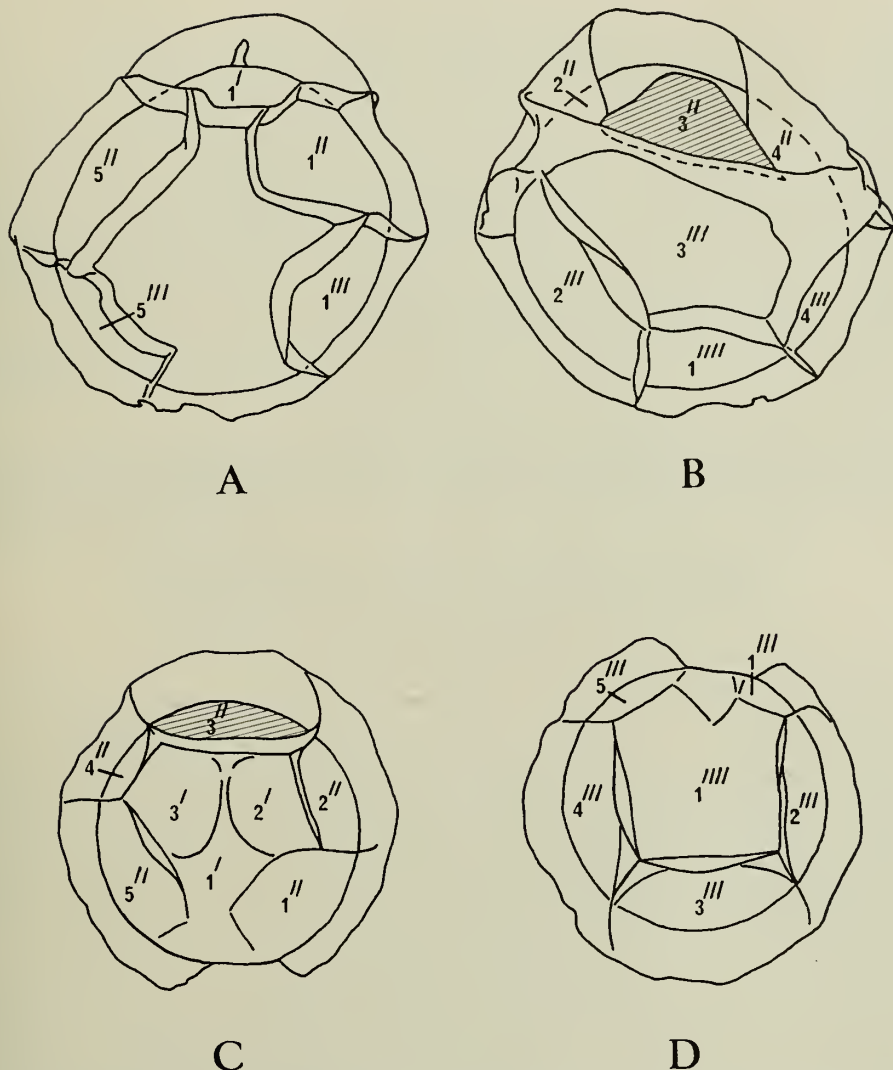


FIG. 17. *Pentadinium laticinctum* Gerlach 1961. A, B. Ventral and dorsal views respectively. V.57750 (4); W32. C, D. Apical and antapical views respectively. V.57752; W37. The precingular archaeopyle (3'') is indicated by shading.

Genus **PENTADINIUM** Gerlach 1961
Pentadinium laticinctum Gerlach 1961

Fig. 17; Pl. 13, figs 6–11

1961 *Pentadinium laticinctum* Gerlach : 165; pl. 26, figs 5–6; text-figs 6–7.

DESCRIPTION. The overall cyst shape is rounded polygonal to subspherical.

Endophragm spherical or subspherical, thick-walled with an irregularly granular surface; surrounding periphragm thin, its surface smooth or granular. Plate boundaries marked by linear thickenings of the periphragm, sutural crests with undulating or irregular distal margins or linear folds in the periphragm. Reflected tabulation 1-3', 5'', 5''', 1'''. The apical zone is usually occupied by a single large polygonal plate, although occasionally three plates are distinguishable (Fig. 17C). A short apical projection may be present at the apical pole (Fig. 17A). The pre-cingular and postcingular zones are separated by a single sutural crest, which is slightly helicoid and is interrupted by the sulcal zone. The sulcal zone is broadest where its boundaries meet the cingular crest (Fig. 17A). The archaeopyle is pre-cingular, formed by the displacement of plate 3''.

DIMENSIONS. Observed range: overall $56 \times 56 \mu$ to $74 \times 78 \mu$; endophragm $48 \times 48 \mu$ to $62 \times 62 \mu$. ($n = 8$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Middle and Upper Oligocene of north Germany (Gerlach 1961, Benedek 1972); Middle Miocene of north Germany (Gerlach 1961).

Genus **POLYSPHAERIDIUM** Davey & Williams 1966b

Polysphaeridium subtile Davey & Williams 1966b

Pl. 14, figs 1-2

1966b *Polysphaeridium subtile* Davey & Williams: 92; pl. 11, fig. 1.

DIMENSIONS. Observed range: diameter of cyst body $36-50 \mu$; length of processes up to 15μ . ($n = 12$).

REMARKS. Specimens here assigned to *P. subtile* frequently exhibit an epittractal archaeopyle. In the generic diagnosis of *Polysphaeridium* the archaeopyle is described as being apical with an angular margin, when present (Davey & Williams 1966b: 92). In the original diagnosis and description of *P. subtile* (the type species of *Polysphaeridium*) no mention is made of the position and form of the archaeopyle. The holotype (Davey & Williams 1966b: pl. 11, fig. 1) appears to show a breakage splitting the cyst body into two halves, suggesting an epittractal archaeopyle. On the basis of this evidence the diagnoses of *Polysphaeridium* and *P. subtile* should be emended to include reference to the epittractal archaeopyle. This would render *Hemicystodinium* Wall 1967 a junior synonym of *Polysphaeridium* since the former genus is also characterized by an epittractal archaeopyle and numerous processes. All the other species at present assigned to *Polysphaeridium* on the basis of their having an apical archaeopyle would then require assignment to a new genus with one of these species as the genotype. These taxonomic changes have not been effected here since none of the other species attributed to *Polysphaeridium* by Davey & Williams (1966b) was recorded in this study.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene and Lower Eocene of northern Spain (Caro 1973); Lower Eocene of the London Basin in southern England (Davey & Williams 1966b, Gruas-Cavagnetto 1970c*).

Genus *SAMLANDIA* Eisenack 1954

Samlandia chlamydotheca Eisenack 1954

Pl. 15, fig. 3

1954 *Samlandia chlamydotheca* Eisenack: 76; pl. 11, figs 12-15.

DIMENSIONS. Observed range: overall $74 \times 50 \mu$ to $110 \times 80 \mu$; endophragm $54 \times 44 \mu$ to $80 \times 78 \mu$; height of pillars up to 10μ ; length of apical horn up to 20μ . ($n = 15$).

REMARKS. The periphragm forms relatively thick, striated pillars or ridges whose distribution over the cyst body results in the formation of a series of circular or polygonal fields. The pillars are distally united by a thin membrane. A simple precingular archaeopyle is frequently recognizable.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1972*) and of north Germany (Morgenroth 1966a); Upper Eocene of north Germany (Agelopoulos 1967) and of East Prussia (Eisenack 1954); Middle Oligocene of north Germany (Benedek 1972).

Genus *SPINIFERITES* Mantell 1850 emend. Sarjeant 1970

Spiniferites ramosus (Ehrenberg) Mantell 1854

Pl. 14, figs 3-7

1838 *Xanthidium ramosum* Ehrenberg: pl. 1, figs 1-2, 5.

1854 *Spiniferites ramosus* (Ehrenberg) Mantell: fig. 77, nos 4, 6.

1932 *Hystrichosphaera ramosa* (Ehrenberg) O. Wetzel: 144.

REMARKS. Specimens here attributed to *Spiniferites ramosus* exhibit a considerable range of variation in process length, development of membrane between the processes, and surface ornament. This has been expressed by Davey & Williams (1966a) in their description of several varieties of *S. ramosus* (as *Hystrichosphaera ramosa*), of which the following are here recognized.

Spiniferites ramosus var. *ramosus* Davey & Williams 1966a

Pl. 14, fig. 3

Spiniferites ramosus var. *granomembraneus* Davey & Williams 1966a

Pl. 14, fig. 5

Spiniferites ramosus var. *granosus* Davey & Williams 1966a

Pl. 14, fig. 4

Spiniferites ramosus var. *membraneus* (Rossignol) Davey & Williams 1966a

Pl. 14, fig. 7

Spiniferites ramosus var. *multibrevis* Davey & Williams 1966a

Pl. 14, fig. 6

OCCURRENCE. All forms occur in the Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. (*S. ramosus* s.l.) Lower Cretaceous (Valanginian) to Recent, world wide in distribution.

Spiniferites cingulatus (O. Wetzel) Sarjeant 1970

Pl. 14, fig. 11

1933 *Cymatiosphaera cingulata* O. Wetzel: 28; pl. 4, fig. 10.

1954 *Hystrichosphaera cingulata* (O. Wetzel) Deflandre: 258.

1970 *Spiniferites cingulatus* (O. Wetzel) Sarjeant: 76.

DIMENSIONS. Observed range: diameter of cyst body $46\text{--}56\ \mu$; height of crests up to $16\ \mu$. ($n = 4$).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Cretaceous (Albian) to Pleistocene – see Davey & Verdier (1971).

Spiniferites cornutus (Gerlach) Sarjeant 1970

Pl. 14, fig. 10

1961 *Hystrichosphaera cornuta* Gerlach: 180; pl. 27, figs 10–12.

1970 *Spiniferites cornutus* (Gerlach) Sarjeant: 76.

DIMENSIONS. Observed range: cyst body $52 \times 40\ \mu$ to $56 \times 56\ \mu$; length of processes up to $13\ \mu$; length of apical horn up to $24\ \mu$. ($n = 3$).

OCCURRENCE. Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1968) and of the Hampshire and London Basins in southern England (Davey & Williams 1966a); Upper Eocene of north Germany (Agelopoulos 1967); Middle Oligocene of north Germany (Gerlach 1961, Benedek 1972); Upper Oligocene of north Germany (Benedek 1972); Middle Miocene of north Germany (Gerlach 1961).

Spiniferites monilis (Davey & Williams) Sarjeant 1970 emend. herein

Pl. 14, figs 8–9

1966a *Hystrichosphaera monilis* Davey & Williams: 45; pl. 5, fig. 2.

1970 *Spiniferites monilis* (Davey & Williams) Sarjeant: 76.

EMENDED DIAGNOSIS. A species of *Spiniferites* with a spherical or subspherical cyst body and a smooth or finely granular surface. Processes short, simple or branched; distally simple or furcate. Furcations taeniate, simple or branched, their distal margin entire, aculeate or secate.

DIMENSIONS. Observed range: diameter of cyst body $21\text{--}44\ \mu$; length of processes up to $12\ \mu$. ($n = 14$).

REMARKS. Davey & Williams (1966a) considered the presence of granules concentrated along the plate boundaries to be a characteristic feature of *S. monilis*. Examination of the holotype and morphologically similar forms from the Bracklesham Beds indicates that the 'sutural ornamentation' in fact consists of small depressions or pits, the development of which is a secondary effect probably due to the presence of pyrite (Neves & Sullivan 1964). As well as being concentrated along the plate boundaries, the pits may occupy large areas on the surface of the cyst body, while in other specimens there is no pit development. This secondary 'ornamentation' effect has also been observed in other taxa, and does not constitute a means of taxonomic distinction. However, *S. monilis* is still a morphologically distinct and valid species.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of the Hampshire and London Basins in southern England (Davey & Williams 1966a).

Spiniferites pseudofurcatus (Klumpp) Sarjeant 1970

Pl. 14, figs 12–13

- 1953 *Hystrichokibotium pseudofurcatum* Klumpp : 388 ; pl. 16, figs 12–14.
 1960 *Hystrichosphaera tertiaria* Eisenack & Gocht : 515 ; text-fig. 4.
 1966a *Hystrichosphaera buccina* Davey & Williams : 42 ; pl. 4, fig. 1, text-figs 10–11.
 1969 *Hystrichosphaera pseudofurcata* (Klumpp) Gocht : 32 ; pl. 4, figs 12–13 ; text-fig. 22.
 1970 *Spiniferites pseudofurcatus* (Klumpp) Sarjeant : 76.
 1970 *Spiniferites buccinus* (Davey & Williams) Sarjeant : 75.

DIMENSIONS. Observed range: diameter of cyst body 45–61 μ ; length of processes up to 30 μ . (n = 7).

REMARKS. The taxonomic problems concerning this species have been discussed by Morgenroth (1966a), Gocht (1969) and Sarjeant (1970). Wall (1967: 103) considered the tabulation pattern of *Hystrichosphaera tertiaria* Eisenack & Gocht 1960 (a junior synonym of *S. pseudofurcatus*) to be typically 'gonyaulacid', and not as originally described by Eisenack & Gocht 1960. This removes the only significant difference between this species and *Spiniferites buccinus* (Davey & Williams) Sarjeant 1970, and the latter species is also considered to be a junior synonym of *S. pseudofurcatus*.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Morgenroth 1966a, as *Hystrichosphaera incerta* ; De Coninck 1965, 1967*, as *Hystrichosphaera tertiaria*, doubtful attributions ; De Coninck 1968, as *Hystrichosphaera* cf. *tertiaria*), of northern France (Gruas-Cavagnetto 1970b, as *Hystrichosphaera buccina*), of north Germany (Morgenroth 1966a, as *Hystrichosphaera incerta* ; Gocht 1969) and of the Hampshire and London Basins in southern England (Davey & Williams 1966a, Downie, Husain & Williams 1971, both as *Hystrichosphaera buccina*) ; Middle Eocene of north Germany (Agelopoulos 1967, as *Hystrichosphaera furcata* and *H. tertiaria* ; Gocht 1969) ; Upper Eocene of north Germany (Klumpp 1953, also as *Areoligera incerta* and *Hystrichosphaera furcata* ; Agelopoulos 1967, as *Hystrichosphaera furcata* and *H. tertiaria*), of East Prussia (Eisenack 1954, as *Hystrichosphaera* cf. *furcata* ; Eisenack & Gocht 1960, as *Hystrichosphaera tertiaria*) ; ? Upper Eocene of north Germany (Gocht 1969) ; Eocene, undifferentiated, of Argentina (Archangelsky 1968, 1969*, as *Hystrichosphaera buccina*, doubtful attributions) ; Middle Oligocene of north Germany (Maier 1959, as *Areoligera* cf. *incerta* ; Gerlach 1961, also as *Hystrichosphaera furcata* ; Benedek 1972) ; questionably from the Middle Oligocene of north Germany (Gocht 1969) ; Upper Oligocene of north Germany (Gerlach 1961, also as *Hystrichosphaera furcata* ; Brosius 1963, as *Hystrichosphaera tertiaria* ; Benedek 1972) ; Middle Miocene of north Germany (Maier 1959, as *Areoligera* cf. *incerta* ; Gerlach 1961, also as *Hystrichosphaera furcata*) ; Miocene–Pliocene of Italy (Habib 1971, as *Spiniferites* sp.).

Genus *THALASSIPHORA* Eisenack & Gocht 1960

Eisenack & Gocht (1960) described *Thalassiphora* as consisting of a spherical or ellipsoidal central body (endophragm) surrounded by a bowl-shaped membrane (periphragm), implying that a large opening is present on the ventral surface of the periphragm in the type species, *Thalassiphora pelagica* (Eisenack) Eisenack & Gocht 1960. The majority of the specimens here assigned to *T. pelagica* also exhibit this large opening on the ventral surface, but in a few forms the small central body appears to be completely surrounded by periphragm on the ventral and dorsal surfaces.

Gocht (1968: pl. 25; 1969: text-fig. 46) illustrated his interpretation of the development of *T. pelagica*, based on material from the Eocene and Middle Oligocene of north Germany. He suggested that in its initial stages *T. pelagica* consists of a thick-walled central body (endophragm) closely surrounded by the periphragm in which linear folds and thickenings define a reflected tabulation of 1', 1a, 5'', 4''', 1''''; Lf (Gocht 1968: pl. 25, figs 1-2; 1969: text-fig. 46a-b). At this stage the overall morphology is totally removed from that of the 'typical' *T. pelagica*. Through a series of intermediate stages the periphragm becomes ventrally concave and develops a ventral opening in the area of the longitudinal furrow (Lf), exposing the endophragm. The periphragm becomes well separated from the endophragm apart from the contact zone on the mid-dorsal surface, and the folds and thickenings which mark the plate boundaries become less clearly defined. The periphragm peels away to form a folded margin in the peripheral zone of the ventral surface, leaving a large opening which occupies nearly all the ventral surface of the cyst (Gocht 1968: pl. 25, figs 3-9; 1969: text-fig. 46c-e). At this stage the cyst attains the 'typical' morphology of *T. pelagica*.

The overall form of *Thalassiphora delicata* Williams & Downie 1966c emend. herein is very similar to that of *T. pelagica*. Three beautifully preserved specimens from the Upper Eocene part of the Bracklesham Beds exhibit a reflected tabulation of 4', 1a, 5'', 4c, 5''', 1p, 1''''', and indicate that *T. delicata* is a dorsoventrally flattened cavate dinoflagellate cyst with several unusual characteristics (Figs 18, 20; Pl. 15, figs 3-5). The thin-walled relatively small central body is completely surrounded by the delicate periphragm, but the two layers are separated by a distinct pericoel except over the mid-dorsal area. The plate boundaries are defined by narrow thickenings of the periphragm, but they are absent from the area where the periphragm and endophragm are in contact. Most of the ventral surface of the periphragm is occupied by plates 1'' and 2''', and the sulcal zone is displaced well to the left of the mid-ventral line. The large ventral opening in the periphragm noted in *T. pelagica* is also present in *T. delicata*, and in the latter species represents plate 1''. The significance of this opening has not been determined. It is difficult to envisage the displacement of this plate area being involved in archaeopyle formation since a 'conventional' dorsal precingular archaeopyle (3'') is developed in the endophragm and periphragm.

Although the described reflected tabulations of *T. pelagica* and *T. delicata* differ, the dorsal surface of *T. pelagica* (Gocht 1968: pl. 27, figs 2c, 3a; 1969: text-fig. 47)

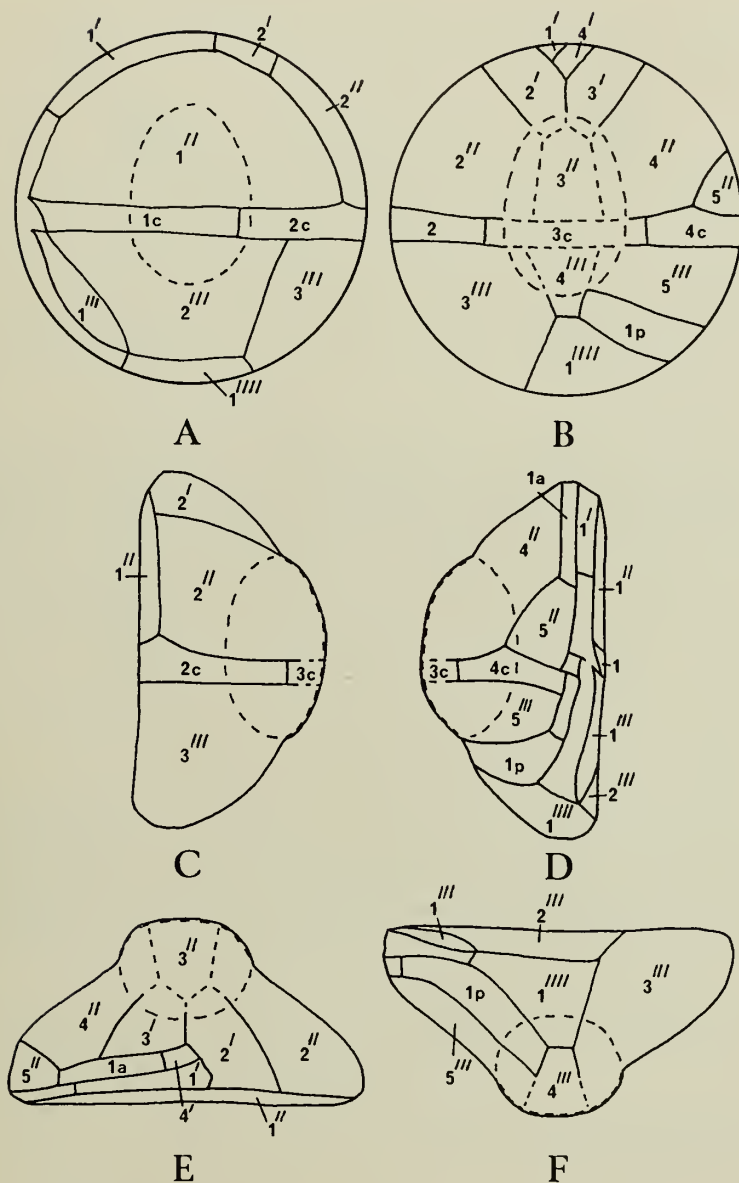


FIG. 18. *Thalassiphora delicata* Williams & Downie 1966c emend. Diagrammatic representation of reflected tabulation. A. Ventral view. B. Dorsal view. C, D. Lateral views. E. Apical view. F. Antapical view. The central body (endophragm) is indicated by the broken line; plate boundaries represented by broken lines are inferred.

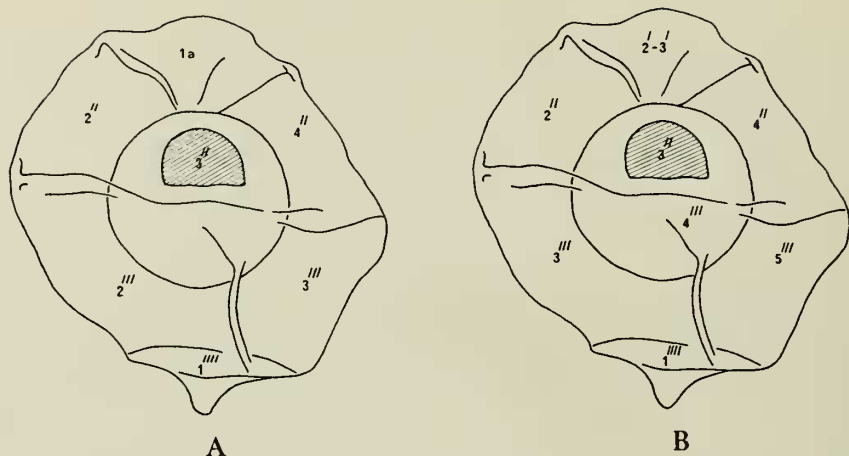


FIG. 19. *Thalassiphora pelagica* (Eisenack) Eisenack & Gocht 1960. Reflected tabulation of dorsal surface. A. Interpretation from Gocht (1968 : pl. 27, fig. 3a ; 1969 : text-fig. 47). B. Interpretation based on reflected tabulation of *Thalassiphora delicata* Williams & Downie 1966c emend. The precingular archaeopyle (3') is represented by shading.

can be interpreted in terms of the reflected tabulation of *T. delicata* (Fig. 19). On this basis, the forms described by Gocht as initial and intermediate stages in the development of *T. pelagica* should be excluded from this species, and I agree with Drugg (1970 : 819) that some of these forms should be included in *Muratodinium* Drugg 1970.

If the concept of *Thalassiphora* is restricted to the original definition by Eisenack & Gocht (1960), together with the possible definition of plate areas, then the species assigned to *Thalassiphora*, e.g. *T. pelagica*, *T. delicata* and *T. reticulata* Morgenroth 1966b, exhibit a considerable range of texture and structure of the periphragm and endophragm. In this respect *T. pelagica* appears to be more closely related to forms such as *Muratodinium* and *Adnatosphaeridium* ? *patulum* Williams & Downie 1966c than to *T. delicata*, but in terms of the present accepted treatment of fossil dinoflagellate cyst taxa this relationship would be at supra-generic level.

Thalassiphora pelagica (Eisenack) Eisenack & Gocht 1960

Fig. 19 ; Pl. 16, figs 4-5

- 1938 *Bion pelagicum* Eisenack : 187 (*nom. nud.*).
 1954 *Pterospermopsis pelagica* Eisenack : 71 ; pl. 12, figs 17-18.
 1960 *Thalassiphora pelagica* (Eisenack) Eisenack & Gocht : 513 ; text-figs 1-3.

DIMENSIONS. Observed range : periphragm $108 \times 126 \mu$ to $212 \times 176 \mu$; endophragm $60 \times 66 \mu$ to $98 \times 94 \mu$; length of keel up to 20μ . ($n = 9$).

REMARKS. Specimens here assigned to *T. pelagica* are dorsoventrally flattened and have a relatively thick-walled central body. The periphragm has a fibro-reticulate appearance, and is separated from the endophragm by a distinct pericoel

except over the mid-dorsal surface where the two layers are in contact. A small projection or 'keel' is developed in the periphragm at the antapex. In addition to the dorsal precingular archaeopyle (3''), a large opening is usually developed in the periphragm occupying most of the ventral surface.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Maastrichtian) of Denmark (Wilson 1971); Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1972*), of northern France (Gruas-Cavagnetto 1970b, doubtful attribution), of north Germany (Morgenroth 1966a, Gocht 1968, 1969) and of the London Basin in southern England (Williams & Downie 1966c); Middle Eocene of northern France (Gruas-Cavagnetto 1971*) and of north Germany (Agelopoulos 1967, Gocht 1968, 1969); Upper Eocene of north Germany (Alberti 1961, as *Pterospermopsis* cf. *pelagica*; Agelopoulos 1967) and of East Prussia (Eisenack 1938, 1954, Eisenack & Gocht 1960); ? Upper Eocene of north Germany (Gocht 1968, 1969); Eocene, undifferentiated, of Argentina (Archangelsky 1968, 1969*), of Chile (Cookson & Cranwell 1967) and of Romania (Balteş 1969, as *T. delicata*); Middle Oligocene of north Germany (Gerlach 1961, Gocht 1968, 1969, Benedek 1972); Upper Oligocene of north Germany (Brosius 1963, Benedek 1972); ? Upper Oligocene of north Germany (Gerlach 1961); Oligocene, undifferentiated, of north Germany (Weiler 1956, as *Pterospermopsis* cf. *danica*) and of Romania (Balteş 1969, as *T. delicata*); Middle Miocene of north Germany (Gerlach 1961).

***Thalassiphora delicata* Williams & Downie 1966c emend. herein**

Figs 18, 20; Pl. 16, figs 1-3

1966c *Thalassiphora delicata* Williams & Downie: 235; pl. 26, fig. 8.

EMENDED DIAGNOSIS. Central body subspherical or ellipsoidal, formed by the thin smooth endophragm.Periphragm dorsoventrally flattened with a subcircular or elliptical outline, smooth or with a minutely fenestrate appearance.Periphragm separated from the endophragm by a distinct pericoel, except over the mid-dorsal area where the two layers are in contact. Low simple linear thickenings of the periphragm are variably developed, and these define the plate boundaries. Reflected tabulation 4', 1a, 5'', 4c, 5''', 1p, 1''''; archaeopyle precingular, formed by displacement of plate 3''. Distribution of the plates strongly asymmetrical. Most of the ventral surface is occupied by plates 1'' and 2'''. Sulcal zone offset well to the left of the mid-ventral line, occupying the lateral margin of the periphragm. A large opening is usually developed on the ventral surface of the periphragm, formed by displacement of plate 1''.

DIMENSIONS. Observed range: periphragm $75 \times 62 \mu$ to $112 \times 120 \mu$; endophragm $36 \times 30 \mu$ to $60 \times 46 \mu$. ($n = 12$).

REMARKS. *T. delicata* shows a variable development of linear thickenings of the periphragm defining the reflected tabulation. In some specimens only the cingular zone and a few of the other plate boundaries are recognizable; in others all the

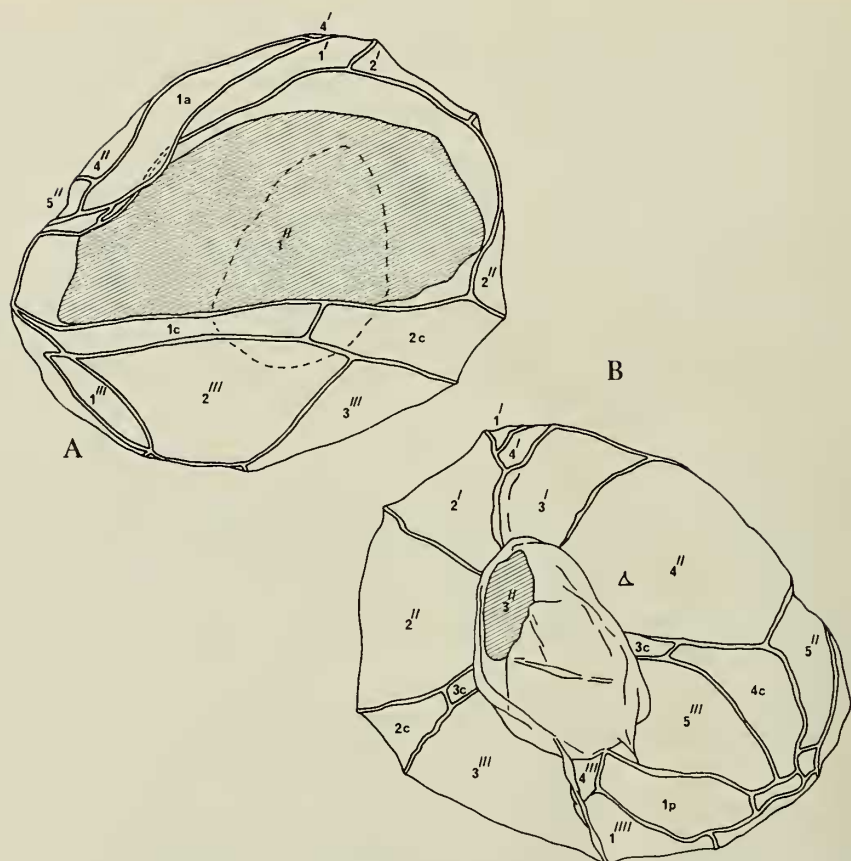


FIG. 20. *Thalassiphora delicata* Williams & Downie 1966c emend., reflected tabulation. A. Ventral view. The central body (endophragm) is indicated by the broken line; shading indicates the large ventral opening representing most of plate 1''. B. Dorsal view; the precingular archaeopyle (3'') is represented by shading. V.57766 (9); W56.

plates are clearly defined apart from those on the mid-dorsal area where the periphragm and endophragm are in contact (Figs 18B, 20B). There is some uncertainty in the reflected tabulation of the area where the sulcal zone crosses the cingular zone. The periphragm in this area frequently exhibits folds which tend to obscure the plate boundaries. Two small plate areas have been recognized which may include the anterior sulcal plate. A large posterior intercalary plate (1p) is developed to the left of the sulcal zone, bordered by plates 4''', 5''' and 1'''. The development of a full reflected tabulation on the ventral surface allows the recognition of its unusual asymmetry, and the identification of the area of the large opening.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Pastiels 1948, as *Spore* inc. sed. Type-spécimen no. 3; De Coninck 1968, 1972*) and of the Hampshire and London

Basins in southern England (Williams & Downie 1966c) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) ; Pleistocene of Norfolk, England (subsurface, presumably as reworking, Wall & Dale 1968b*).

Genus *TURBIOSPHAERA* Archangelsky 1968

In the original diagnosis of *Turbiosphaera*, Archangelsky (1968 : 408) defined the reflected tabulation as 1', 6'', 6c, 6''', (1p), 1''', with plate 1' reflected by a large process or apical horn. In the two species here assigned to this genus the apical horn shows considerable proximal expansion. Although it could not be confirmed, these proximal expansions may well include apical processes situated around, and proximally united with, the apical horn.

Turbiosphaera galatea n. sp.

Pl. 15, figs 4-6

DERIVATION OF NAME. Greek Γαλάτεια, a sea nymph.

DIAGNOSIS. Cyst body subcircular or oval in outline. Apical horn and delicate intratabular processes formed by the fibrous periphragm. Processes vary from discrete, with an undulating distal margin, to typically vague, due to their delicate appearance and the development of fibrous proximal membrane. They show considerable variation in breadth. Processes reflect the precingular, cingular, postcingular and antapical zones. Antapical process similar in form to the other processes, but longer, and proximally united with the postcingular processes. Apical horn broad, triangular in form, and showing considerable proximal expansion. Fibrous proximal membrane frequently unites processes in adjacent tabulation zones. Archaeopyle precingular, formed by displacement of plate 3''.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57783 (4). Sample AB11, bed 2g, Bracklesham Beds, Lower Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: overall $115 \times 84 \mu$; cyst body $75 \times 63 \mu$; length of processes up to 19μ ; length of apical horn 23μ ; length of antapical process 22μ . Observed range: overall $104 \times 68 \mu$ to $130 \times 84 \mu$; cyst body $60 \times 44 \mu$ to $80 \times 75 \mu$; length of processes up to 20μ ; length of apical horn up to 30μ ; length of antapical process up to 26μ . ($n = 10$).

REMARKS. The considerable proximal expansion of the apical horn may include apical processes. The delicate appearance and typically vague definition of the processes precludes the determination of their exact number. When discrete processes are developed there appears to be one broad process per plate area, and more than one process per plate area when the processes are slender. The delicacy of its processes and the form of its apical horn distinguish *T. galatea* n. sp. from *T. filosa* (Wilson) Archangelsky 1968.

OCCURRENCE. Lower Eocene.

Turbiosphaera magnifica n. sp.

Pl. 15, figs 7-9

DERIVATION OF NAME. Latin, *magnificus*, magnificent.

DIAGNOSIS. Cyst body subcircular or oval in outline. Apical horn and intratabular processes formed by the fibrous periphragm. Processes variable in breadth, with an undulating distal margin. There is one process per reflected plate area. Apical horn long, broad-based, triangular in form and showing considerable proximal expansion. Pre- and postcingular processes typically flattened parallel to the long axis of the cyst body. Cingular processes flattened parallel to the short axis of the cyst body. Cingular zone slightly helicoid. Antapical process longer than the other processes, distally expanded, and frequently showing a short distal projection. Very slender processes may be present between the primary precingular and cingular processes. Precingular processes situated close to, and sometimes united with, the proximal expansions of the apical horn. Postcingular processes situated close to, and proximally united with, the antapical process. Reflected tabulation 1', 6'', 6c, 5''', 1''''; archaeopyle precingular, formed by displacement of plate 3''.

HOLOTYPE. B.M.(N.H.) Palaeont. Slide V.57756 (7). Sample W40, bed 11, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: overall $144 \times 62 \mu$; cyst body $74 \times 46 \mu$; length of processes up to 26μ ; length of apical horn 38μ ; length of antapical process 36μ . Observed range: overall $110 \times 62 \mu$ to $148 \times 80 \mu$; cyst body $56 \times 46 \mu$ to $80 \times 62 \mu$; length of processes up to 34μ ; length of apical horn up to 48μ ; length of antapical process up to 38μ . ($n = 10$).

REMARKS. The considerable proximal expansion of the apical horn may include apical processes. The development of very slender processes between the primary precingular and cingular processes is also a feature of Forma F of Evitt (1961: 392; pl. 6, figs 1-5; pl. 7, figs 1-2). The close affinity between the latter form and *Turbiosphaera filosa* has been noted by Wilson (1967a: 66) and Archangelsky (1968: 410). The processes are arranged in three discrete groups: apical horn and precingular processes, cingular processes, antapical and postcingular processes. This feature and the form of its apical horn distinguishes *T. magnifica* n. sp. from *T. filosa* (Wilson) Archangelsky 1968 and *T. galatea* n. sp. It is further distinguished from *T. galatea* by having a longer apical horn and more clearly defined processes.

OCCURRENCE. Middle Eocene.

PERIDINIACEAN GROUP

Genus *DEFLANDREA* Eisenack 1938 emend. Williams & Downie 1966c

Deflandrea phosphoritica Eisenack 1938

Pl. 17, fig. 1

1938 *Deflandrea phosphoritica* Eisenack: 187; fig. 6.

DIMENSIONS. Observed range : periphragm, length 80–132 μ , breadth 72–100 μ ; endophragm, length 50–78 μ , breadth 60–84 μ . ($n = 24$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*) and of Russia (Alberti 1959); Lower Eocene of Belgium (Reisinger 1950, Morgenroth 1966a, Gruas-Cavagnetto 1968), of northern France (Chateauneuf & Gruas-Cavagnetto 1968*), of north Germany (Morgenroth 1966a, Gocht 1969), of northern Spain (Caro 1973), of Russia (Alberti 1959) and of the Hampshire and London Basins in southern England (Williams & Downie 1966c, Downie, Husain & Williams 1971); ? Lower Eocene of Victoria, Australia (Deflandre & Cookson 1955); Middle Eocene of north Germany (Agelopoulos 1967, Gocht 1969); Upper Eocene of Belgium (Rozen 1965), of East Prussia (Eisenack 1938, 1954), of northern France (Chateauneuf & Gruas-Cavagnetto 1968*), of north Germany (Klumpp 1953, Alberti 1959, Agelopoulos 1967), of the Hampshire Basin (Gruas-Cavagnetto 1970a*) and of Victoria (Cookson & Eisenack 1965); ? Upper Eocene of north Germany (Gocht 1969); Eocene, undifferentiated, of Romania (Baltes 1969), of Russia (Alberti 1959) and of Western Australia (Cookson & Eisenack 1961); Upper Eocene–Lower Oligocene of Russia (Chiguryaeva 1956, as Algae ? (Peridineae); Vozzhennikova 1967); Lower Oligocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*); Middle Oligocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*) and of north Germany (Maier 1959, Alberti 1959, Gerlach 1961, Gocht 1969, Benedek 1972); Upper Oligocene of north Germany (Maier 1959, Alberti 1959, Gerlach 1961, Brosius 1963, Benedek 1972); Oligocene, undifferentiated, of Romania (Baltes 1969); Lower Tertiary, undifferentiated, of Russia (Alberti 1959), of Spitzbergen (Manum 1960) and of Tierra del Fuego, Argentina (Baldis 1966); Miocene, undifferentiated, of Romania (Baltes 1967*).

Deflandrea depressa Morgenroth 1966a

Pl. 16, fig. 6

1966a *Deflandrea depressa* Morgenroth : 8; pl. 1, fig. 2.

DESCRIPTION. A single specimen of *D. depressa* has been recorded in this study. The periphragm and endophragm are very thin. The epitrectal portion of the periphragm tapers from the cingular zone to form a large apical horn; the antapical margin of the periphragm is produced into two distinct horns. The helicoid cingular zone is best defined on the ventral surface; horns ornamented with a sparse covering of fine granules and the area of the periphragm in contact with the endophragm crossed by numerous delicate longitudinal wrinkles.

DIMENSIONS.Periphragm, length 70 μ , breadth 32 μ ; endophragm, length 32 μ , breadth 32 μ . ($n = 1$).

OCCURRENCE. Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of north Germany (Morgenroth 1966a), of Belgium (De Coninck 1968, 1972*) and of northern France (Chateauneuf & Gruas-Cavagnetto 1968*).

Deflandrea wetzeli Morgenroth 1966a

Pl. 17, fig. 4

1966a *Deflandrea wetzeli* Morgenroth : 9 ; pl. 1, figs 4-5.

DESCRIPTION. Outline of periphragm broadly oval, modified by the development of a short apical horn and two short antapical horns.Periphragm ornamented with short blunt or acuminate projections, which may be proximally united on the margins of the cingular zone. Apart from the area immediately below the horns, the endophragm lies very close to, or in contact with, the periphragm.

DIMENSIONS. Observed range : periphragm, length 46-88 μ , breadth 35-60 μ ; endophragm, length 31-56 μ , breadth 35-56 μ . ($n = 36$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of north Germany (Morgenroth 1966a) and of Belgium (Pastiels 1948, as *Peridinium* cf. *galeatum* - pl. 5, fig. 17 only ; De Coninck 1968).

Genus *KISSELEVIA* Vozzhennikova 1967

In the original description of this genus (as *Kisselovia* nom. nud.), Vozzhennikova (1963) noted the presence of an internal body. In a later paper (Vozzhennikova 1967), however, she considered this statement erroneous and stated that no internal body was present. Examination of her illustration of *Kisselevia ornata* (Vozzhennikova 1967 : pl. 43, fig. 1) and the specimens here assigned to *K. insolens* n. sp. suggests that an outer periphragm and an inner capsule (endophragm) are distinguishable. The reticulate 'armour' which is characteristic of the genus consists of a complex mesh of interconnected trabeculae distally uniting the short processes distributed over the periphragm. In *K. insolens* n. sp. this attains the appearance of a fenestrate membrane. In the latter species only the dorsal surface reflected tabulation has been determined and this is clearly peridiniacean.

Confirmation of the separation of the periphragm and endophragm in the Russian species of *Kisselevia* would suggest a close affinity between this genus and *Wetzeliella* Eisenack 1938 emend. Williams & Downie 1966b. This would favour the establishment of *Kisselevia* as a subgenus of *Wetzeliella* to accommodate existing species of *Kisselevia* and species now assigned to *Wetzeliella* (*Wetzeliella*) Eisenack 1938 in which the processes are distally united by membranes or trabeculae (e.g. *W. (W.) tenuivirgula* Williams & Downie 1966b).

Kisselevia insolens n. sp.

Pl. 18, figs 1-2

DERIVATION OF NAME. Latin, *insolens*, odd, strange, with reference to the unusual fenestrate 'shell' which distally unites the processes in this species.

DIAGNOSIS. Overall outline rounded pentagonal or rounded tetragonal. Periphragm produced into five horns, one apical, two lateral and two antapical. Right antapical horn typically slightly shorter than the left. Separation of the periphragm and endophragm may be distinguishable at the base of each horn. Thick short processes are developed over the periphragm, and arranged in simulate complexes. Processes in each complex are distally united by a thick strong fenestrate membrane whose outline and area are similar to those of the underlying plate. Fenestrations in the membrane variable in size and shape (circular, subcircular or rounded polygonal). Adjacent areas of fenestrate membrane united by thick bars. The resulting outer layer has the appearance of a strong fenestrate 'shell'. Reflected tabulation of the form 4', 3a, 7'', 5''', 2''''; archaeopyle intercalary, formed by displacement of plate 2a.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57774 (4). Sample AB₄, bed 2c, Bracklesham Beds, Lower Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: overall $118 \times 115 \mu$. Observed range: overall $112 \times 112 \mu$ to $148 \times 134 \mu$. ($n = 4$).

REMARKS. Although the basic reflected tabulation in *K. insolens* n. sp. is considered to be comparable to that of *Wetzeliella* Eisenack 1938 emend. Williams & Downie 1966b, only the dorsal surface reflected tabulation has been precisely determined. The cingular zone is not marked by areas of fenestrate membrane; the areas of membrane over the pre- and postcingular zones are united across the cingular zone by thick bars. The presence of a strong fenestrate outer 'shell' distinguishes *K. insolens* from described species of *Kisselevia* which are characterized by the presence of a relatively delicate network of distal trabeculae. *K. insolens* does show some overall similarity to the single specimen attributed to *Wetzeliella* (*W.*) *tenuivirgula* var. *crassoramosa* Williams & Downie 1966b in this study, but in the latter form the processes are distally united by a network of extremely thick trabeculae rather than a fenestrate 'shell'.

OCCURRENCE. Lower Eocene.

Genus **LEJEUNIA** Gerlach 1961

Lejeunia hyalina Gerlach 1961

Pl. 17, fig. 5

1961 *Lejeunia hyalina* Gerlach: 169; pl. 26, figs 10–11.

DIMENSIONS. Observed range: overall $56 \times 62 \mu$ to $100 \times 108 \mu$. ($n = 6$).

REMARKS. The only tabulation features observed are the cingular zone and a poorly defined sulcal zone indicated by folds or thickenings of the cyst wall, and a simple archaeopyle on the dorsal surface which appears to be intercalary in position.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Palaeocene of Russia (Vozzhennikova 1967); Lower Eocene of Belgium (De Coninck 1968) and of north Germany (Gocht 1969); Middle Oligocene of north Germany (Benedek 1972); Upper Oligocene of north Germany (Gerlach 1961).

Genus *PALAEOCYSTODINIUM* Alberti 1961

Palaeocystodinium golzowense Alberti 1961

Pl. 16, fig. 7

1961 *Palaeocystodinium golzowense* Alberti : 20 ; pl. 7, figs 10–12 ; pl. 12, fig. 16.

DIMENSIONS. Observed range : overall length of periphragm 156–220 μ ; endophragm 60 $\times$ 25 μ to 64 $\times$ 50 μ . (n = 4).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Maastrichtian) and ? Palaeocene of Gabon, west Africa (Malloy 1972) ; Palaeocene of South Dakota, U.S.A. (Stanley 1965) ; Lower Eocene of Belgium (De Coninck 1968, 1972*) and of France (Gruas-Cavagnetto 1970b*) ; Upper Eocene of north Germany (Alberti 1961) ; Middle Oligocene of north Germany (Alberti 1961, Benedek 1972) ; Upper Oligocene of north Germany (Alberti 1961, Brosius 1963, as *Netrellytron* sp. ; Benedek 1972).

Genus *PHTHANOPERIDINIUM* Drugg & Loeblich 1967

The genus was originally defined by Drugg & Loeblich (1967). The type species, *P. amoenum* Drugg & Loeblich 1967, from the Oligocene of Mississippi, U.S.A., has a basic reflected tabulation of 4', 3a, 7'', 5c, 5''', 1'''' and subdivision of the sulcal zone. Three new species of *Phthanoperidinium* are here recorded – *P. alectrolophum*, *P. echinatum* and *P. tritonium*. No indication of individual plate areas has been recognized in the cingular and sulcal zones of these, the reflected tabulation being 4', 3a, 7'', 5''', 1'''' (Fig. 21). Three other described taxa from Palaeogene sediments are here transferred to the genus *Phthanoperidinium* on the basis of their overall morphology and reflected tabulation :

Phthanoperidinium comatum (Morgenroth 1966b) n. comb. = *Peridinium comatum* Morgenroth 1966b : 1 ; pl. 1, figs 1–2. Lower Oligocene, north Germany.

Phthanoperidinium eocenicum (Cookson & Eisenack 1965) n. comb. = *Peridinium eocenicum* Cookson & Eisenack 1965 : 119 ; pl. 11, figs 1–5. Upper Eocene, Victoria, Australia.

Phthanoperidinium resistente (Morgenroth 1966a) n. comb. = *Peridinium resistente* Morgenroth 1966a : 5 ; pl. 2, figs 1–2. Lower Eocene, north Germany.

Three species assigned to *Hystrichogonyaulax* Sarjeant 1969 by Benedek (1972) – *Hystrichogonyaulax* sp., *H. coreoides* and *H. polytrix*, recorded from the Middle Oligocene of north Germany – are possibly referable to *Phthanoperidinium* on the basis of their morphology and probable archaeopyle position. However, the reflected tabulation of *H. coreoides* as described by Benedek (1972) does not conform with that of *Phthanoperidinium*, while in *Hystrichogonyaulax* sp. and *H. polytrix* the reflected tabulation has not been determined.

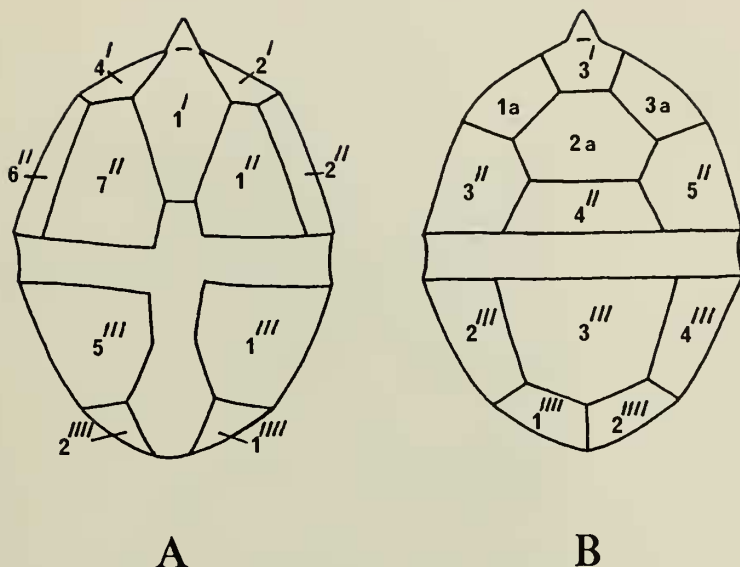


FIG. 21. Diagrammatic representation of the reflected tabulation of *Phthanoperidinium* Drugg & Loeblich 1967 as exhibited by forms from the Bracklesham Beds. A. Ventral view. B. Dorsal view.

***Phthanoperidinium alectrolophum* n. sp.**

Fig. 23A; Pl. 17, figs 10–11

DERIVATION OF NAME. Greek ἀλεκτορόλοφος, cockscomb, with reference to the form of the sutural crests.

DIAGNOSIS. Cyst body has a smooth surface, and a subcircular or rounded polygonal outline modified by a short blunt apical horn. Plate boundaries marked by thin smooth sutural crests of variable height. Undulating distal margin of crests frequently thickened, bearing numerous short solid spines. Cingular zone clearly defined, and slightly helicoid. Reflected tabulation 4', 3a, 7'', 5''', 2''''; archaeopyle intercalary, formed by displacement of plate 2a.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57791 (13). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: overall $59 \times 48 \mu$; height of crests up to 7μ ; length of spines up to 2μ . Observed range: overall $40 \times 30 \mu$ to $60 \times 56 \mu$; height of crests up to 7μ ; length of spines up to 2μ . ($n = 6$).

REMARKS. The sutural crests in *Phthanoperidinium alectrolophum* n. sp. are similar in form to those of *P. campoense* Caro 1973 (incorrectly cited as *Phtanoperidinium*) and *P. eocenicum* (Cookson & Eisenack 1965) n. comb. In *P. campoense* the crests are described as being surmounted by short irregularly distributed projections, as opposed to the relatively dense regular spine distribution in *P. alectrolophum*. The crests in *P. eocenicum* do not show a distal thickening, and their distal

SUCCESSION			TAXA	
			<i>Achilleodinium bifurmoides</i> <i>Achomosphaera alicornu</i> <i>A. membraniphora</i> <i>A. ramulifera</i> <i>Adactosphaeridium multispinosum</i> <i>A. robustum</i> <i>A. vittatum</i> <i>Araeosphaera araneosa</i> <i>Arealigera coronata</i> <i>A. cf. coronata</i> <i>A. meduselliformis</i> <i>A. cf. meduselliformis</i> <i>A. senanensis</i> <i>A. cf. senanensis</i> <i>A. sentosa</i> <i>A. taulona</i> <i>A. undulata</i> <i>Araeosphaeridium arcuatum</i> <i>A. diktyoplokus</i> <i>A. multicornutum</i> <i>Canosphaeropsis</i> <i>Chiropteridium cf. dispersum</i> <i>Cordosphaeridium</i> <i>C. fibrospinosum</i> <i>C. gracilis</i> <i>C. inodes</i> <i>C. minimum</i> <i>C. multispinosum</i> <i>Cyclonophidium divaricatum</i> <i>C. exuberans</i> <i>C. cf. exuberans</i>	
CLAYS	19	c	58	
		b	57	
		a	56	
		a	55	
SAND - ROCK	18	a	54	
SANDY CLAYS	17	a	53	
		a	52	
SANDS	16	a	51	
		a	50	
		a	49	
		a	48	
SANDS	15	a	47	
SANDY CLAYS	14	a	46	
SANDS	13	a	45	
SANDY CLAYS	12	a	44	
		a	43	
LAMINATED BEDS	11	a	42	
		a	41	
		a	40	
		a	39	
GREENSANDS	10	b	38	
		b	37	
		b	36	
		b	35	
		a	34	
		a	33	
		a	32	
		a	31	
		a	30	
		a	29	
LAMINATED BEDS	9	c	28	
		b	28A	
		a	27	
		a	26A	
LIGNITE & UNDERCLAY	8	a	26	
		a	25B	
LAMINATED BEDS	7	a	25A	
		a	25	
GREENSAND	6	a	24	
		a	23	
SANDY CLAYS	5	a	22A	
		a	22	
		a	21	
		a	20	
LAMINATED BEDS	4	a	19	
		a	18	
		a	17	
		a	16	
LAMINATED BEDS	3	a	15	
		a	14	
		a	13	
		a	12	
		a	11	
		a	10	
		a	9	
		a	8	
SANDY CLAYS	2	a	7	
		a	6	
		a	5	
		a	4	
		a	3	
		a	2	
SANDY CLAYS	1	a	1	
		a	1	
		a	1	
		a	1	

FIG. 22. Distribution of dinoflagellate cyst taxa assigned to the Gonyax

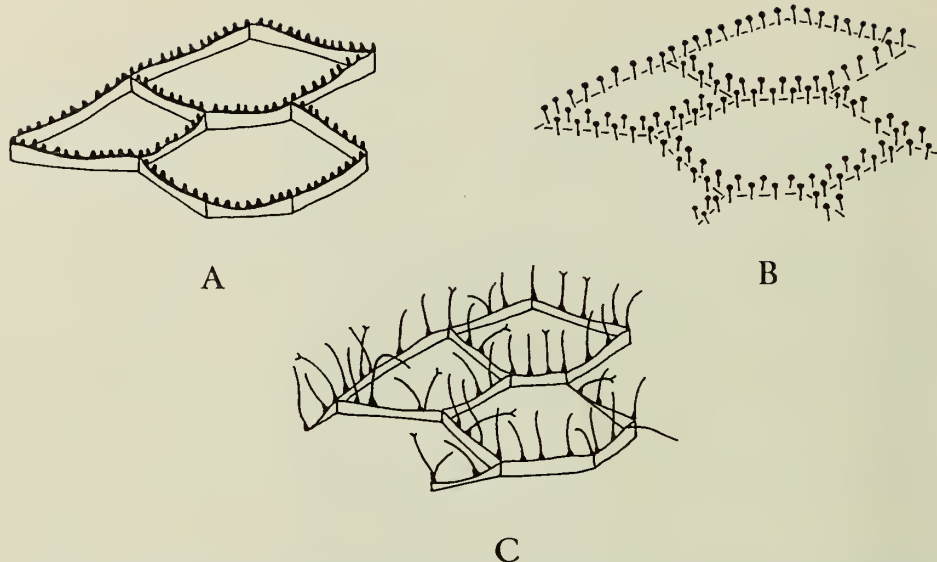


FIG. 23. Diagrammatic representation of the ornament in three new species of *Phthanoperidinium*. A. *P. alectrolophum* n. sp. B. *P. echinatum* n. sp. C. *P. tritonium* n. sp.

margin is described as being ornamented with evenly spaced granules and small tubercles, or sparsely denticulate. This species is further distinguished from *P. alectrolophum* by the presence of an antapical horn.

OCCURRENCE. Upper Eocene.

***Phthanoperidinium echinatum* n. sp.**

Fig. 23B; Pl. 17, figs 8–9, 12

DERIVATION OF NAME. Latin, *echinatus*, prickly, spiny, with reference to the form of the spinate ornament.

DIAGNOSIS. Cyst body has a smooth surface, and a subcircular or rounded polygonal outline modified by a short blunt apical horn. Plate boundaries accentuated by a distinctive ornament concentrated at the plate margins, consisting of short hair-like projections, each with a bulbous spherical distal termination. Cingular zone clearly defined and slightly helicoid. Reflected tabulation 4', 3a, 7'', 5''', 2''''; archaeopyle intercalary, formed by displacement of plate 2a.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57755 (4). Sample W39, bed 10b, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: overall $29 \times 22 \mu$; length of spines up to 2μ . Observed range: overall $26 \times 22 \mu$ to $48 \times 42 \mu$; length of spines up to 3μ . ($n = 26$).

REMARKS. The majority of the recorded specimens are complete or exhibit an intercalary archaeopyle formed by the displacement of plate 2a. A few specimens

have been observed with plate 4'' displaced as well as plate 2a, probably due to sutural weakness. The distinctive ornament of *P. echinatum* distinguishes this species from all described species of *Phthanoperidinium*.

OCCURRENCE. Lower, Middle and Upper Eocene.

***Phthanoperidinium tritonium* n. sp.**

Figs 23C, 24; Pl. 17, figs 2-3, 6-7

DERIVATION OF NAME. Latin, *Triton*, a sea god.

DIAGNOSIS. Cyst body has a smooth surface, and a subcircular or rounded polygonal outline modified by a short blunt apical horn. Plate boundaries marked by thin smooth sutural crests of variable height, bearing erect or curved solid spines which may be distally simple or bifurcate. Circular zone clearly defined and distinctly helicoid. Reflected tabulation 4', 3a, 7'', 5''', 2''''; archaeopyle intercalary, formed by displacement of plate 2a.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57756 (14). Sample W40, bed 11, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body $44 \times 37 \mu$; length of spines up to 7μ . Observed range: cyst body $30 \times 26 \mu$ to $56 \times 46 \mu$; length of spines up to 13μ . ($n = 22$).

REMARKS. In some specimens, in addition to plate 2a (the operculum), plate 4'' is also displaced (Pl. 17, fig. 7), and in one specimen all three intercalary plates have

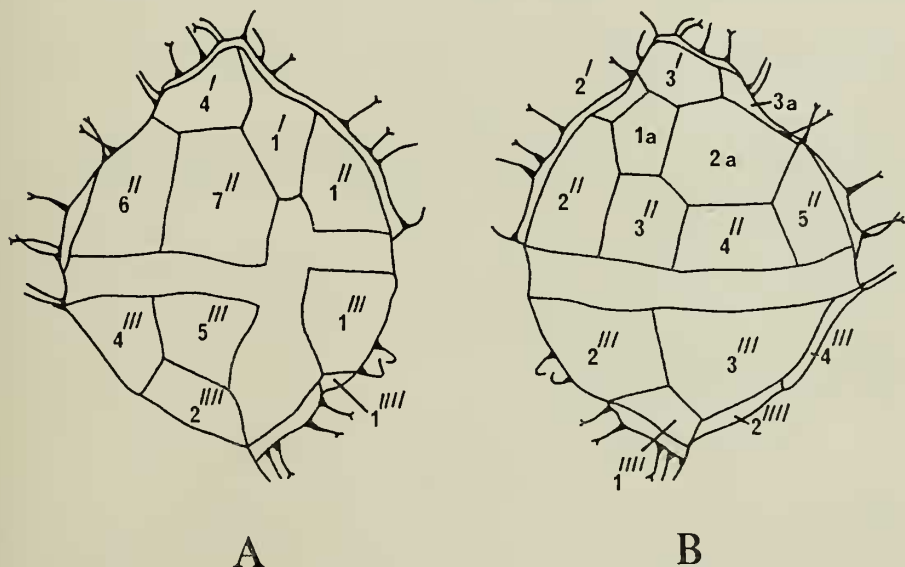


FIG. 24. *Phthanoperidinium tritonium* n. sp. Reflected tabulation of holotype.

A. Ventral view. B. Dorsal view. V.57756 (14); W40.

been lost, probably owing to sutural weakness. In overall form *Phthanoperidinium tritonium* n. sp. is similar to *P. comatum* (Morgenroth 1966b) n. comb., which is distinguished by its consistently longer spines (maximum 28 μ , majority 14–22 μ). The sutural crests in *P. tritonium* are similar to those of *P. alectrolophum* n. sp., though in the latter species the crests bear numerous short simple spines, while in *P. tritonium* they are longer, more widely spaced, and may be distally bifurcate.

OCCURRENCE. Lower, Middle and Upper Eocene.

Genus **WETZELIELLA** Eisenack 1938 emend. Williams & Downie 1966b

Subgenus **WETZELIELLA** Eisenack 1938

Wetzelietta (Wetzelietta) articulata Eisenack 1938

Pl. 18, fig. 3

1938 *Wetzelietta articulata* Eisenack : 186 ; fig. 4.

1961 *Wetzelietta (Wetzelietta) articulata* Eisenack ; Alberti : 7.

DIMENSIONS. Observed range : periphragm 78 $\times$ 78 μ to 164 $\times$ 164 μ ; endophragm 66 $\times$ 64 μ to 102 $\times$ 102 μ . (n = 40).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene of Victoria, Australia (Cookson 1956, doubtful attribution) ; Uppermost Palaeocene of north Germany (Alberti 1961) ; Palaeocene–Lower Eocene of New Zealand (Wilson 1967c, 1968a*) ; Lower Eocene of Belgium (De Coninck 1965, 1967*, 1972* ; Morgenroth 1966a), of northern France (Chateauneuf & Gruas-Cavagnetto 1968, Gruas-Cavagnetto 1970b*), of north Germany (Alberti 1961, Morgenroth 1966a), of northern Spain (Caro 1973) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b) ; Middle Eocene of north Germany (Klumpp 1953, Agelopoulos 1967) ; Upper Eocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968), of north Germany (O. Wetzel 1935, as *Peridinium* sp. indet. ; Klumpp 1953, Alberti 1961, Agelopoulos 1967), of East Prussia (Eisenack 1938, 1954) and of Russia (Alberti 1961, Vozzhennikova 1967) ; ? Upper Eocene of north Germany (Gocht 1969) ; Lower Oligocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968) and of Russia (Vozzhennikova 1967) ; Middle Oligocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968) and of north Germany (Alberti 1961, Gerlach 1961, Gocht 1969) ; Upper Oligocene of north Germany (Alberti 1961, Gerlach 1961, Brosius 1963) ; ? Middle Miocene of north Germany (Gerlach 1961).

Wetzelietta (Wetzelietta) coleothrypta Williams & Downie 1966b

Pl. 18, fig. 4

1966b *Wetzelietta (Wetzelietta) coleothrypta* Williams & Downie : 185 ; pl. 18, figs 8–9 ; text-fig. 47.

DIMENSIONS. Observed range : periphragm 100 $\times$ 84 μ to 150 $\times$ 146 μ ; endophragm 60 $\times$ 50 μ to 116 $\times$ 98 μ . (n = 21).

REMARKS. In typical forms the processes in each simulate complex are distally united by a thin membrane similar in outline and area to the underlying plate. Other specimens show a reduction in the areas of distal membrane. These forms appear to be transitional to *W. (W.) clathrata* Eisenack 1938 in which adjacent processes are distally united by narrow ribbons or 'lists'.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of New Zealand (Wilson 1967c), of northern Spain (Caro 1973) and of the London Basin in southern England (Williams & Downie 1966b, Downie, Husain & Williams 1971); Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

***Wetziella (Wetziella) condylos* Williams & Downie 1966b**

Pl. 18, fig. 5

1966b *Wetziella (Wetziella) condylos* Williams & Downie : 193; pl. 20, figs 1-2.

DIMENSIONS. Observed range: periphragm $74 \times 86 \mu$ to $100 \times 100 \mu$; endophragm $54 \times 60 \mu$ to $76 \times 80 \mu$. ($n = 4$).

REMARKS. The periphragm forms short reduced lateral and antapical horns. The curved apical margin is sometimes developed into a low apical horn.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Lower Eocene of the London Basin in southern England (Williams & Downie 1966b, Downie, Husain & Williams 1971).

***Wetziella (Wetziella) homomorpha* Deflandre & Cookson 1955**

Pl. 19, fig. 1

1955 *Wetziella homomorpha* Deflandre & Cookson : 254; pl. 5, fig. 7; text-fig. 19.

1966a *Wetziella (Wetziella) homomorpha* Deflandre & Cookson; Morgenroth : 10; pl. 1, figs 8-9.

DIMENSIONS. Observed range: overall (including processes) $66 \times 60 \mu$ to $85 \times 86 \mu$; periphragm $46 \times 44 \mu$ to $78 \times 74 \mu$. ($n = 15$).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene of New Zealand (Wilson 1967c), of Tasmania (Cookson & Eisenack 1967a), of northern France (Chateauneuf & Gruas-Cavagnetto 1968) and of northern Spain (Caro 1973); Lower Eocene of Belgium (Pastiels 1948, as *Hystrichosphaeridium geometricum*; De Coninck 1965, 1967*, 1968, 1972*, Morgenroth 1966a, Gruas-Cavagnetto 1968), of northern France (Gruas-Cavagnetto 1968, 1970b, Chateauneuf & Gruas-Cavagnetto 1968), of north Germany (Morgenroth 1966a), of northern Spain (Caro 1973), of the Hampshire and London Basins in southern England (Williams & Downie 1966b, Downie, Husain & Williams 1971*) and of Victoria, Australia (Deflandre & Cookson 1955); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); Upper Eocene, and Lower and Middle Oligocene

of northern France (Chateauneuf & Gruas-Cavagnetto 1968); ? Oligocene of Victoria (Cookson 1953, as *Hystriosphæridium geometricum*).

***Wetzeliiella (Wetzeliiella) lunaris* Gocht 1969**

Pl. 19, fig. 2

1969 *Wetzeliiella (Wetzeliiella) lunaris* Gocht: 13; pl. 10, figs 1-3; text-fig. 6.

DIMENSIONS. Observed range: periphragm $78 \times 74 \mu$ to $146 \times 140 \mu$; endophragm $54 \times 56 \mu$ to $90 \times 84 \mu$. ($n = 12$).

REMARKS. In *W. (W.) lunaris* four of the five horns are well developed – the apical, two lateral and the left antapical. The right antapical horn is considerably reduced. The endophragm is subcircular to rounded tetragonal in outline, and its margin is always separated from the periphragm by a narrow pericoel.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Pastiels 1948, as *Hystriosphæridium articulatum*, pl. 4, figs 13, 17 only; De Coninck 1965, as *W. articulata*, pl. 1, figs 3-6 only; Gruas-Cavagnetto 1968, as *W. articulata*), of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b, as *W. (W.) symmetrica* var. *lobisca*; Downie, Husain & Williams 1971).

***Wetzeliiella (Wetzeliiella) meckelfeldensis* Gocht 1969**

Pl. 19, fig. 5

1969 *Wetzeliiella (Wetzeliiella) meckelfeldensis* Gocht: 15; pl. 10, figs 12-15.

DIMENSIONS. Observed range: periphragm $78 \times 78 \mu$ to $166 \times 150 \mu$; endophragm $58 \times 54 \mu$ to $98 \times 92 \mu$. ($n = 6$).

REMARKS. In *W. (W.) meckelfeldensis* only four horns are developed – one apical, two lateral, and a single antapical horn which is slightly offset to the left when viewed from the dorsal surface. The endophragm has an oval outline, and apart from the area at the base of each horn, it is typically in contact with the periphragm.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Lower Eocene of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b, as *W. (W.) symmetrica*; Downie, Husain & Williams 1971); Middle and ? Upper Eocene of north Germany (Gocht 1969).

***Wetzeliiella (Wetzeliiella) reticulata* Williams & Downie 1966b**

Pl. 19, fig. 3

1966b *Wetzeliiella (Wetzeliiella) reticulata* Williams & Downie: 187; pl. 19, figs 3, 6; text-fig. 48.

DIMENSIONS. Observed range: periphragm $108 \times 102 \mu$ to $140 \times 144 \mu$; endophragm $74 \times 74 \mu$ to $102 \times 108 \mu$. ($n = 5$).

REMARKS. In *W. (W.) reticulata* the processes are mainly arranged in simulate complexes. The processes in each complex are distally united by a complicated network of fine trabeculae, the resulting net being similar in outline and area to the underlying plate area.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORD. Lower Eocene of the London Basin in southern England (Williams & Downie 1966b).

***Wetzelietta (Wetzelietta) similis* Eisenack 1954**

Pl. 19, fig. 4

1954 *Wetzelietta similis* Eisenack : 58 ; pl. 8, figs 8–10.

1966b *Wetzelietta (Wetzelietta) similis* Eisenack ; Williams & Downie : 194 ; pl. 20, fig. 5.

DIMENSIONS. Observed range : periphragm $78 \times 84 \mu$ to $116 \times 108 \mu$; endophragm $54 \times 60 \mu$ to $72 \times 70 \mu$. ($n = 11$).

REMARKS. Specimens here assigned to *W. (W.) similis* have a broad low apical horn, two distinct lateral horns, a distinct left antapical horn and a much reduced right antapical horn. The endophragm is subcircular in outline, relatively thick walled, and typically granular.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1972*) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b) ; Middle and Upper Eocene of north Germany (Agelopoulos 1967) ; Upper Eocene of East Prussia (Eisenack 1954).

***Wetzelietta (Wetzelietta) tenuivirgula* Williams & Downie 1966b**

Pl. 20, figs 1–2

1966b *Wetzelietta (Wetzelietta) tenuivirgula* Williams & Downie : 188 ; pl. 19, figs 2, 4 ; text-fig. 49.

DIMENSIONS. Observed range : periphragm $72 \times 78 \mu$ to $164 \times 162 \mu$; endophragm $54 \times 40 \mu$ to $122 \times 114 \mu$. ($n = 13$).

REMARKS. In *W. (W.) tenuivirgula* the majority of the processes are arranged in simulate complexes. Adjacent processes in each complex are distally united by thin trabeculae. Additional distal trabeculae may also develop crossing the complexes, and giving the appearance of a loose open net, which, however, never attains the complexity exhibited in *W. (W.) reticulata*. Specimens here assigned to *W. (W.) tenuivirgula* show considerable variation in the length of the horns (Pl. 20, figs 1, 2).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*), of northern Spain (Caro 1973) and of the London Basin in southern England (Williams & Downie 1966b ; Downie, Husain & Williams 1971*).

***Wetzeliiella (Wetzeliiella) tenuivirgula* var. *crassoramosa* Williams & Downie 1966b**

Pl. 20, fig. 3

1966b *Wetzeliiella (Wetzeliiella) tenuivirgula* var. *crassoramosa* Williams & Downie : 189 ; pl. 19, figs 1, 5, 7 ; text-fig. 50.

DIMENSIONS. Overall $102 \times 108 \mu$. ($n = 1$).

REMARKS. A single specimen is here attributed to this distinctive variety of *W. (W.) tenuivirgula*. The processes are distally united by extremely thick trabeculae, but the latter do not attain the appearance of the outer 'shell' developed in *Kisselevia insolens* n. sp. (p. 292).

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Lower Eocene of the Hampshire and London Basins in southern England (Williams & Downie 1966b ; Downie, Husain & Williams 1971).

***Wetzeliiella (Wetzeliiella) varielongituda* Williams & Downie 1966b**

Pl. 20, fig. 4

1966b *Wetzeliiella (Wetzeliiella) varielongituda* Williams & Downie : 196 ; pl. 20, figs 4, 8.

DIMENSIONS. Observed range : periphragm $72 \times 78 \mu$ to $164 \times 162 \mu$; endophragm $54 \times 40 \mu$ to $122 \times 114 \mu$. ($n = 13$).

REMARKS. *W. (W.) varielongituda* is characterized by a subtetragonal outline, a broad low apical horn, and reduced lateral and antapical horns. The endophragm is subcircular in outline and thick walled.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1972*), of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b ; Downie, Husain & Williams 1971*) ; Middle Eocene of north Germany (Gocht 1969) ; Upper Eocene - Lower Oligocene of Russia (Vozzhennikova 1967).

Subgenus ***RHOMBODINIUM*** Gocht 1955

Gocht's (1955) genus *Rhombodinium* was made a subgenus of *Wetzeliiella* Eisenack 1938 by Alberti (1961).

***Wetzeliiella (Rhombodinium) glabra* (Cookson) Vozzhennikova 1967**

Pl. 20, fig. 5

1956 *Wetzeliiella glabra* Cookson : 186 ; pl. 2, figs 1-5.

1967 *Rhombodinium glabra* (Cookson) Vozzhennikova : 169.

DIMENSIONS. Observed range : periphragm $130 \times 132 \mu$ to $140 \times 150 \mu$; endophragm $66 \times 66 \mu$ to $74 \times 80 \mu$. ($n = 3$).

REMARKS. The specimens here assigned to *W. (R.) glabra* are closely comparable to those recorded from the Lower Eocene of southern England by Williams &

Downie (1966b). They differ from the type material (Eocene of South Australia ; Cookson 1956) in having a reduced apical horn and only one distinct antapical horn (left). The right antapical horn is represented by a slight bulge in the periphragm. Wilson (1967c) suggested that the European forms may represent a separate species. However, Morgenroth (1966a) illustrated a specimen (pl. 1, fig. 12) which is intermediate between the Australasian and the European forms (Morgenroth 1966a : pl. 1, fig. 11), suggesting that *W. (R.) glabra* can exhibit a considerable range of morphological variation.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Morgenroth 1966a) and of the London Basin in southern England (Williams & Downie 1966b) ; Upper Eocene of New Zealand (Wilson 1967c) ; Eocene, undifferentiated, of South Australia (Cookson 1956).

UNKNOWN AFFINITIES GROUP

Genus *HETERAULACACYSTA* Drugg & Loeblich 1967

Heteraulacacysta ? leptalea n. sp.

Pl. 21, figs 1-2

DERIVATION OF NAME. Greek λεπτάλεος, fine, delicate, with reference to the overall appearance of this species.

DIAGNOSIS. Cyst body has a smooth or punctate surface, and a subcircular or elliptical outline in polar view.Periphragm wrinkled and folded, forming low simple crests which define the apical and antapical zones, and at least five plate areas in both the pre- and postcingular zones. Cingular zone bordered by two broad membranous crests with undulating distal margins. Circular fenestrations frequently developed in the proximal area of the cingular crests, along with fine elongate fenestrations aligned at right-angles to the margin of the cyst body. Cingular crests reduced across the sulcal zone.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57766 (8). Sample W56, bed 19c, Bracklesham Beds, Upper Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype : overall (polar view) $106 \times 90 \mu$; cyst body (polar view) $76 \times 66 \mu$; height of cingular crests up to 18μ . Observed range : overall mean diameter (polar view) $71-100 \mu$; mean diameter of cyst body (polar view) $53-72 \mu$; height of cingular crests up to 18μ . ($n = 10$).

REMARKS. All the specimens here assigned to *H. ? leptalea* n. sp. only show a polar view which is comparable to that of *H. campanula* Drugg & Loeblich 1967, the type species of *Heteraulacacysta*. However, as the full reflected tabulation and the mode of archaeopyle formation have not been determined in *H. ? leptalea*, the generic assignment is tentative. Small perforations in the periphragm, comparable to those present in the proximal area of the cingular crests, frequently give a punctate appearance to the surface of the cyst body. *H. ? leptalea* differs from

H. campanula Drugg & Loeblich 1967 in having generally poorly developed low sutural crests, a frequently punctate rather than positively ornamented surface to the cyst body, and in exhibiting circular and elongate fenestrations in the cingular crests.

OCCURRENCE. Middle and Upper Eocene.

Genus **IMPLETOSPHAERIDIUM** Morgenroth 1966a

There is considerable variation in the overall form of the solid processes in species assigned to this genus (Fig. 24). Basically they are either rod-like and circular or subcircular in cross-section, or consist of erect membranes with variable distal terminations. Apart from the occasional presence of a polygonal opening which is probably an archaeopyle, no definite indications of reflected tabulation have been observed.

***Impletosphaeridium cracens* n. sp.**

Fig. 25E; Pl. 21, fig. 6

DERIVATION OF NAME. Latin, *cracens*, graceful, with reference to the form of the processes.

DIAGNOSIS. Cyst body spherical or subspherical, with a smooth surface. Processes numerous, consisting of erect membranes of variable breadth, strengthened by rod-like thickenings. Processes simple or branched, frequently proximally united by lateral extension of the membranes. Distally the processes have a digitate or aculeate margin.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57745 (1). Sample W27, bed 9a, Bracklesham Beds, Lower Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: diameter of cyst body $29\ \mu$; length of processes up to $12\ \mu$. Observed range: diameter of cyst body $18\text{--}30\ \mu$; length of processes up to $13\ \mu$. ($n = 10$).

REMARKS. The membranous processes with their rod-like thickenings distinguish *I. cracens* n. sp. from all described species of *Impletosphaeridium*. *Cordosphaeridium*? *minimum* (Morgenroth) Benedek 1972 also has rod-like thickenings in its processes, but the latter are distinctly tubular, and not erect membranes as in *I. cracens*.

OCCURRENCE. Lower, Middle and Upper Eocene.

***Impletosphaeridium implicatum* Morgenroth 1966a**

Fig. 25A; Pl. 21, fig. 10

1966a *Impletosphaeridium implicatum* Morgenroth: 34; pl. 9, figs 1–3.

1968 *Adnatosphaeridium*? *capitatum* De Coninck: 39; pl. 11, figs 9–13, 21–24; not fig. 14.

DESCRIPTION. The subspherical cyst body bears a dense cover of solid processes which are circular or subcircular in cross-section, simple or branched, with long flexuous distal terminations.

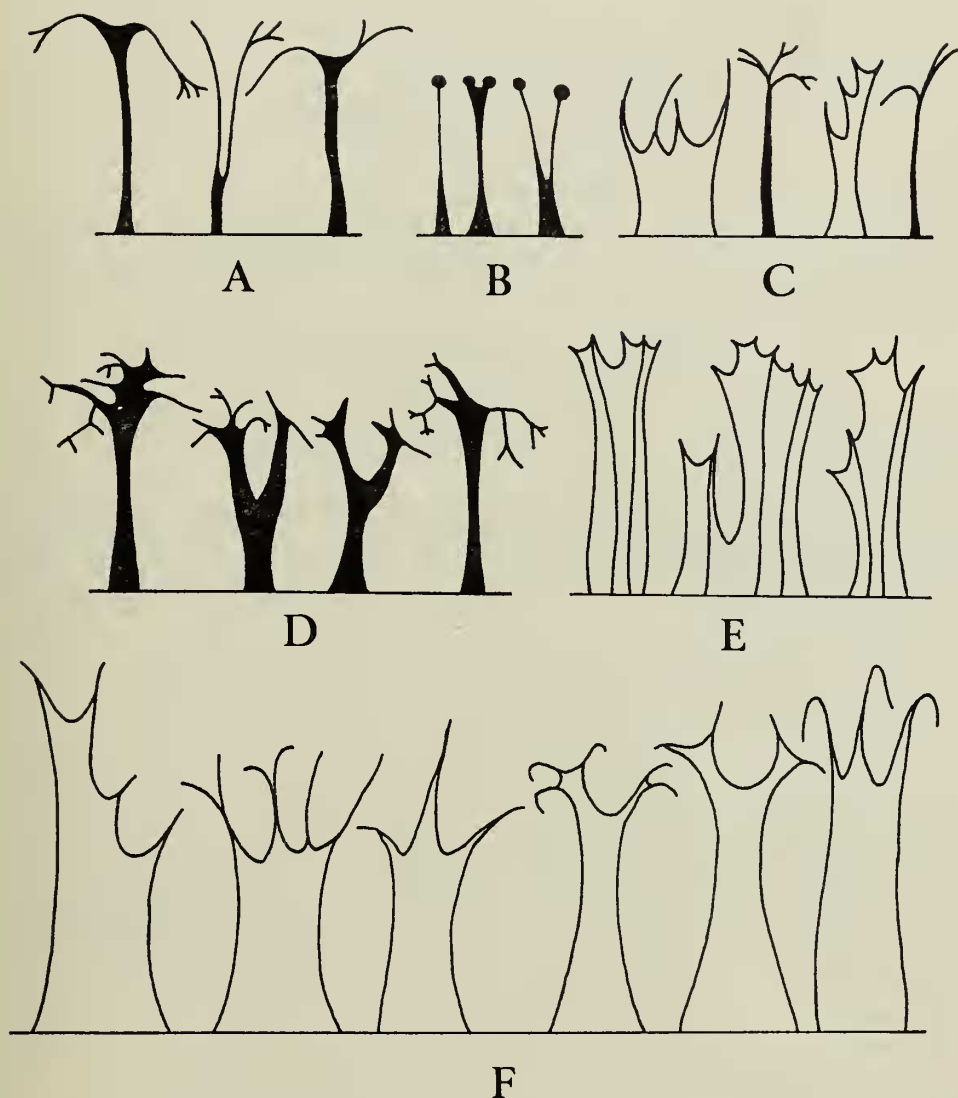


FIG. 25. Diagrammatic representation of process form in *Impletosphaeridium* Morgenroth 1966a. Shaded processes are circular or subcircular in cross-section; unshaded processes are membranous, and 'blade-like' in cross-section. A. *I. implicatum* Morgenroth 1966a. B. *I. insolitum* n. sp. C. *I. kroemmelbeini* Morgenroth 1966a. D. *I. rugosum* Morgenroth 1966a. E. *I. cracens* n. sp. F. *I. luxurium* n. sp.

DIMENSIONS. Observed range: diameter of cyst body $24\text{--}39\ \mu$; length of processes up to $13\ \mu$. ($n = 3$).

REMARKS. Most of the specimens assigned to *Adnatosphaeridium* ? *capilatum* by De Coninck (1968) and Gruas-Cavagnetto (1970) possess the flexuous processes characteristic of *I. implicatum*, although one illustrated by De Coninck (1968: pl. 11, fig. 14) has very short, apparently simple processes; this form is not included here.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of north Germany (Morgenroth 1966a), of Belgium (De Coninck 1968, as *Adnatosphaeridium* ? *capilatum*) and of northern France (Gruas-Cavagnetto 1970b, as *A.* ? *capilatum*).

***Impletosphaeridium insolitum* n. sp.**

Fig. 25B; Pl. 21, figs 5, 8

DERIVATION OF NAME. Latin, *insolitus*, unusual, odd, with reference to the form of the processes.

DIAGNOSIS. Cyst body spherical or subspherical, with a smooth or finely granular surface. Processes numerous, slender and solid. They are simple or bifurcate, with small bulbous spherical or subspherical distal terminations, and may be thickened by the development of proximal membrane; membrane may also be present in the angle of bifurcation.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57759 (13). Sample W51, bed 17, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: diameter of cyst body $22\ \mu$; length of processes up to $9\ \mu$. Observed range: diameter of cyst body $15\text{--}24\ \mu$; length of processes up to $9\ \mu$. ($n = 10$).

REMARKS. Most specimens have simple and bifurcate processes but a few have been observed in which all the processes are simple. The point of bifurcation usually occurs within the distal half of the process. The cyst body occasionally shows a polygonal opening, but no other indications of reflected tabulation have been observed. The unusual form of the processes distinguishes *I. insolitum* n. sp. from all other described species of *Impletosphaeridium*.

OCCURRENCE. Lower, Middle and Upper Eocene.

***Impletosphaeridium kroemmelbeini* Morgenroth 1966a**

Fig. 25C; Pl. 21, fig. 9

1966a *Impletosphaeridium kroemmelbeini* Morgenroth: 34; pl. 9, figs 4–5.

DESCRIPTION. Cyst body spherical or subspherical with two types of processes – some slender and rod-like, circular or subcircular in cross-section, and distally bifurcate or multifurcate; others blade-like, membranous, variable in breadth and branched or digitate, with typically aculeate distal terminations.

DIMENSIONS. Observed range: diameter of cyst body $28-35\ \mu$; length of processes up to $15\ \mu$. ($n = 5$).

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORD. Lower Eocene of north Germany (Morgenroth 1966a).

***Impletosphaeridium luxurium* n. sp.**

Fig. 25F; Pl. 21, figs 3-4

DERIVATION OF NAME. Latin, *luxuria*, excess, with reference to the large number of processes present in this species.

DIAGNOSIS. Cyst body subspherical with a smooth surface. Processes numerous, membranous and of variable breadth. They are bifurcate or digitate with slender aculeate distal terminations.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57791 (12). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: diameter of cyst body $37\ \mu$; length of processes up to $15\ \mu$. Observed range: diameter of cyst body $30-37\ \mu$; length of processes up to $16\ \mu$. ($n = 6$).

REMARKS. The processes in *I. luxurium* n. sp. are similar to the membranous ones in *I. kroemmelbeini* Morgenroth 1966a. *I. luxurium* is usually distinguished, however, by having broader processes, and does not exhibit the slender rod-like ones which are present in *I. kroemmelbeini*.

OCCURRENCE. Middle and Upper Eocene.

***Impletosphaeridium rugosum* Morgenroth 1966a**

Fig. 25D; Pl. 21, fig. 7

1966a *Impletosphaeridium rugosum* Morgenroth: 36; pl. 10, figs 2-3.

DESCRIPTION. Cyst body spherical or subspherical. Processes numerous, solid, and circular or subcircular in cross-section. They are simple or branched and 'tree-like' in overall form, and have slender aculeate distal terminations which may be simple, bifurcate or multifurcate.

DIMENSIONS. Observed range: diameter of cyst body $18-33\ \mu$; length of processes up to $13\ \mu$. ($n = 9$).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORD. Lower Eocene of north Germany (Morgenroth 1966a).

**IV. THE STRATIGRAPHICAL APPLICATION OF DINOFLAGELLATE CYSTS
IN THE BRACKLESHAM BEDS OF THE ISLE OF WIGHT**

a. *Microplankton zonation of the Bracklesham Beds*

The distribution of the 106 microplankton taxa recorded from the Bracklesham Beds of Whitecliff Bay is shown in Figs 22 (p. 296) and 26, and of Alum Bay in Figs 27 and 28. A series of five informal microplankton zones is proposed for the Bracklesham Beds of the Isle of Wight based on the stratigraphical ranges of 70 selected

species, all but two of which are present in both sections. *Lanternosphaeridium lanosum* and *Wetzeliiella* (W.) *tenuivirgula* var. *crassoramosa* were only recorded at Alum Bay. The majority of the selected species have not been recorded from the London Clay of the Isle of Wight, and they are considered to have their stratigraphical inception within the Bracklesham Beds. The remaining species which have been recorded from the London Clay at Whitecliff Bay (Williams 1963, Davey *et al.* 1966a) persist into the Bracklesham Beds but not into the overlying Barton Beds (Bujak 1973). The stratigraphical ranges at Whitecliff Bay and Alum Bay of the selected species are shown in Figs 29 and 30 respectively.

There is a fairly regular appearance of stratigraphically new species through the type section of the Bracklesham Beds at Whitecliff Bay (Fig. 29), and hence the selection of zone boundaries based purely on palaeontological data is somewhat arbitrary. For this reason, and because this is the type section, the informal zone boundaries have been deliberately selected to coincide with significant lithological boundaries.

MICROPLANKTON ZONE 1. Whitecliff Bay: bed 1–bed 4 (Fisher beds I–III); Alum Bay: bed 1–bed 2f.

This zone is characterized by the appearance of 15 species which persist into higher zones of the Bracklesham Beds, but have not been recorded from the London Clay of the Isle of Wight: *Achilleodinium biformoides*, *Adnatosphaeridium vittatum*, *Cyclonephelium vicinum*, *Eocladopyxis peniculatum*, *Homotryblium abbreviatum*, *Hystrichokolpoma granulata*, *Impletosphaeridium implicatum*, *I. insolitum*, *I. rugosum*, *Lanternosphaeridium axiale*, *Phthanoperidinium echinatum*, *Polysphaeridium subtile*, *Samlandia chlamydomphora*, *Wetzeliiella* (W.) *coleothrypta* and *W. (W.) tenuivirgula*.

L. axiale was recorded in this zone at Whitecliff Bay, but at Alum Bay it was not recorded below Zone 2. *S. chlamydomphora* and *I. implicatum* were recorded in this zone at Alum Bay, but at Whitecliff Bay the former species was not recorded below Zone 2, and the latter species not below Zone 3.

This zone is further characterized by the rare occurrence of *Kisselevia insolens*, *Lanternosphaeridium lanosum*, *Wetzeliiella* (R.) *glabra*, *Wetzeliiella* (W.) *condylos* and *W. (W.) reticulata*. None of these species has been recorded above Zone 1, or from the London Clay at Whitecliff Bay, although the last three species are known to occur in the London Clay of the London Basin (Williams & Downie 1966b).

Hystrichosphaeridium tubiferum and *Wetzeliiella* (W.) *similis* are present throughout the London Clay at Whitecliff Bay and both persist into Zone 1 of the Bracklesham Beds. Neither species was recorded in higher zones.

The microplankton assemblages in Zone 1 frequently include numerous examples of the *Areoligera senonensis* complex, forming over 30% of the assemblage at some horizons. Three of the species in this complex (*A. coronata*, *A. medusettiformis* and *A. senonensis*) were not recorded above Zone 1; the other three (*A. cf. coronata*, *A. cf. medusettiformis* and *A. cf. senonensis*) persist into Zone 4, but the complex as a whole does not form a significant proportion of the microplankton assemblages above Zone 1.

The lack of palynological data from the barren Bagshot Sands tends to exaggerate the stratigraphical significance of the appearance of several dinoflagellate cyst

SUCCESSION			TAXA	
			<i>Delandrea depressa</i> <i>D. phosphorilica</i> <i>D. weizelii</i> <i>Kisselevia insolens</i> <i>Lejeunea hyalina</i> <i>Paracystodinium golzowense</i> <i>Phanoperidinium alectrolophum</i> <i>P. echinatum</i> <i>P. tritaniatum</i> <i>Weißeella (W.) glabra</i> <i>Weißeella (W.) articulata</i> <i>W. (W.) calochrypha</i> <i>W. (W.) canalyos</i> <i>W. (W.) hamamapha</i> <i>W. (W.) lunaris</i> <i>W. (W.) meckelfidensis</i> <i>W. (W.) reticulata</i> <i>W. (W.) similis</i> <i>W. (W.) tenuivirgula</i> <i>W. (W.) varrelongiloba</i> <i>Heteraulacacysta?</i> <i>leptalea</i> <i>Impletosphaeridium cracens</i> <i>I. implicatum</i> <i>I. insolitum</i> <i>I. kraemmeri</i> <i>I. luxurium</i> <i>I. rugosum</i>	
CLAYS	19	c	58	
			57	
		b	56	
		a	55	
SAND-ROCK	18		54	
SANDY CLAYS	17		53	
			52	
SANDS	16		51	
			50	
			49	
			48	
SANDS	15		47	
SANDY CLAYS	14		46	
SANDS	13		45	
SANDY CLAYS	12		44	
			43	
			42	
			41	
LAMINATED BEDS	11		40	
			39	
			38	
			37	
GREENSANDS	10	b	36	
			35	
		a	34	
			33	
LAMINATED BEDS	9	c	32	
		b	31	
		a	30	
			29	
LIGNITE & UNDERCLAY	8		28A	
			28	
			27	
			26A	
LAMINATED BEDS	7		26	
			25B	
			25	
			24	
GREENSAND	6		23	
			22A	
			22	
			21	
SANDY CLAYS	5		20	
			19	
			18	
			17	
LAMINATED BEDS	4		16	
			15	
			14	
			13	
SANDS	3		12	
			11	
			10	
			9	
LAMINATED BEDS	2		8	
			7	
			6	
			5	
SANDY CLAYS	1		4	
			3	
			2	
			1	

Fig. 26. Distribution of dinoflagellate cyst taxa assigned to the Peridiniacean and Unknown Affinities Groups in the Bracklesham Beds at Whitecliff Bay, Isle of Wight.

species in the lowest Bracklesham Beds which have not been recorded from the London Clay. If microplankton assemblages from sediments equivalent in age to the Bagshot Sands of the Isle of Wight exist, it is highly likely they will be found to include some of the species which appear in microplankton Zone 1 of the Bracklesham Beds.

MICROPLANKTON ZONE 2. Whitecliff Bay: bed 5–bed 8 (Fisher beds IV–V, in part); Alum Bay: bed 2g. (Although bed 8 (lignite and underclay) at Whitecliff Bay did not yield microplankton, for convenience it is assigned to Zone 2).

This zone is characterized by the appearance of six species which persist into higher zones of the Bracklesham Beds, but were not recorded in Zone 1: *Areosphaeridium diktyoplokus*, *Cyclonephelium laciniiforme*, *C. spinetum*, *Hystriocholpoma salacia*, *Pentadinium laticinctum* and *Turbiosphaera galatea*.

A single specimen of *Wetzeliiella* (W.) *tenuivirgula* var. *crassoramosa* is here recorded from Zone 2 at Alum Bay. This form was recorded from the London Clay at Whitecliff Bay (Williams & Downie 1966b), but was not encountered in Zone 1 of the Bracklesham Beds.

The highest records of *Adnatosphaeridium robustum* and *Cyclonephelium* aff. *exuberans* were noted in Zone 2.

At Alum Bay the upper part of Zone 2 and the lower part of Zone 3 are represented by a palynologically barren interval, bed 3 to bed 8. The only interval positively assignable to Zone 2 is bed 2g which has yielded *C. laciniiforme*, *C. spinetum* and *T. galatea*. *A. diktyoplokus* and *P. laticinctum* first appear in bed 9, the lowest interval positively assignable to Zone 3, and *H. salacia* was not recorded below Zone 5.

MICROPLANKTON ZONE 3. Whitecliff Bay: bed 9a–bed 10a (Fisher beds V, in part, –VI); Alum Bay: bed 9–bed 14c.

This zone is characterized by the appearance of 10 species which persist into higher zones of the Bracklesham Beds, but were not recorded below Zone 3: *Araneosphaera araneosa*, *Areoligera sentosa*, *A. tauloma*, *Chiropteridium* cf. *dispersum*, *Cordosphaeridium* ? *minimum*, *Heteraulacacysta* ? *leptalea*, *Impletosphaeridium cracens*, *I. kroemmelbeini*, *I. luxurium* and *Phthanoperidinium tritonium*.

C. cf. *dispersum*, *H.* ? *leptalea* and *C.* ? *minimum* were recorded in this zone at Whitecliff Bay, but at Alum Bay the first two species were not recorded below Zone 4, and the third species not below Zone 5. *I. luxurium* was recorded in this zone at Alum Bay, but at Whitecliff Bay it was not recorded below Zone 4.

The highest records of *Hystriocholpoma granulata*, *Turbiosphaera galatea* and *Wetzeliiella* (W.) *meckelfeldensis* were noted in Zone 3.

As mentioned above, the lower part of Zone 3 at Alum Bay is represented by palynologically barren sediments.

MICROPLANKTON ZONE 4. Whitecliff Bay: bed 10b–bed 18 (Fisher beds VII–XVI); Alum Bay: bed 14d–e.

This zone is characterized by the appearance of four species which persist into Zone 5 of the Bracklesham Beds, but were not recorded below Zone 4: *Achomosphaera membraniphora*, *Areosphaeridium arcuatum*, *Homotryblidium oceanicum* and

SUCCESSION		TAXA																												
			<i>Deflandrea phosphorilica</i>	<i>D. weitzell</i>	<i>Kisselevia insulensis</i>	<i>Lejeunea hyalina</i>	<i>Palaeocystadinium galzowense</i>	<i>Phidnapteridium oleicrathum</i>	<i>P. echinatum</i>	<i>P. trilineatum</i>	<i>Weitzellia (R.) glabra</i>	<i>Weitzellia (W.) articulata</i>	<i>W. (W.) calechryps</i>	<i>W. (W.) condylas</i>	<i>W. (W.) homomorpha</i>	<i>W. (W.) lunaris</i>	<i>W. (W.) meckelfeldensis</i>	<i>W. (W.) reticulata</i>	<i>W. (W.) similis</i>	<i>W. (W.) tenuivirgula</i>	<i>W. (W.) tenuivirgula var. crassomacosa</i>	<i>W. (W.) varielongiluda</i>	<i>Heteraulacysta? lepidalea</i>	<i>Impletosphaeridium cracens</i>	<i>I. implicatum</i>	<i>I. insolitum</i>	<i>I. kroemmelbeini</i>	<i>I. luxurium</i>	<i>I. rugosum</i>	
SANDY CLAYS	19	44	X				X	X	X		X													X						
		43									X																			
		42	X					X	X	X		X												X	X	X	X	X	X	
		41								X		X																		
		40	X					X	X		X												X	X						
SANDS	18	39																												
CLAYS	17	38																												
CLAYS & LIGNITES	16	37																												
		36																												
SANDS	15	35																												
		34																												
		33																												
		32																												
		31A																												
		31																												
		30																												
		29																												
LAMINATED BEDS	14	d 28	X								X	X								X				X	X					X
		27A																												
		c 27																												
		b 26										X	X																	
		a 25B	X									X	X		X						X									
CLAY	13	25A																												
		25																												
LAMINATED BEDS	12	24C									X			X														X		
		24B	X	X						X											X						X			
CLAY	11	24A																												
SANDS	10	24																												
		23																												
		22																												
LAMINATED BEDS	9	21	X							X	X			X										X				X		
		20									X	X												X			X			
		19									X	X														X				
		18		X	X						X	X															X			
		17B	X								X	X																X		
CLAY	8	17A																					X							
SANDS	7	17																												
PIPECLAY	6	16																												
SAND & PIPECLAYS	5	b 15																												
		a 14A																												
SANDS	4	14																												
SANDS & PIPECLAYS	3	13																												
LAMINATED BEDS	2	g 12								X															X					
		f 11									X																			
		e 10																												
		d 9	X																											

FIG. 28. Distribution of dinoflagellate cyst taxa assigned to the Peridiniacean and Unknown Affinities Groups in the Bracklesham Beds at Alum Bay, Isle of Wight.

Lanternosphaeridium vectense. *H. oceanicum* was recorded in this zone at Whitecliff Bay but at Alum Bay it was not recorded below Zone 5.

Turbiosphaera magnifica was found to be restricted to Zone 4 at Whitecliff Bay and Alum Bay although it was recorded from the Barton Beds at Alum Bay by Bujak (1973).

The highest records of the *Areoligera senonensis* complex, *Chiropteridium* cf. *dispersum*, *Cordosphaeridium fibrospinosum*, *Cyclonephelium divaricatum*, *C. ordinatum*, *Eocladopyxis peniculatum*, *Impletosphaeridium implicatum*, *Membranilarnacia ursulae*, *Wetzeliiella* (W.) *lunaris* and *W. (W.) tenuivirgula* were noted in Zone 4.

At Alum Bay the upper part of Zone 4 and possibly the lowest part of Zone 5 are represented by an interval which is devoid of microplankton, bed 15 to bed 18. The only interval positively assignable to Zone 4 is bed 14d-e, which has yielded three of the four characteristic species appearing in this zone.

MICROPLANKTON ZONE 5. Whitecliff Bay : bed 19a-c (Fisher beds XVII-XIX, in part) ; Alum Bay : bed 19.

This zone is characterized by the appearance of eight species which persist into the overlying Barton Beds (Bujak 1973), but were not recorded below Zone 5 : *Areoligera undulata*, *Areosphaeridium multicornutum*, *Cyclonephelium intricatum*, *Distatodinium craterum*, *D. ellipticum*, *D. paradoxum*, *Hystrichosphaeridium asterium* and *Phthanoperidinium alectrolophum*.

The highest records of *Achomosphaera membraniphora*, *Adnatosphaeridium vittatum*, *Areoligera sentosa*, *Cordosphaeridium exilimurum*, *Cyclonephelium exuberans*, *C. laciniiforme*, *C. spinetum*, *C. vicinum*, *Hystrichokolpoma salacia*, *Hystrichosphaeridium patulum*, *Impletosphaeridium cracens*, *I. luxurium*, *Lanternosphaeridium vectense* and *Wetzeliiella* (W.) *varielongituda* were noted in Zone 5. None of these species was recorded from the Barton Beds (Bujak 1973).

The Bracklesham Beds represent the upper part of the Lower Eocene, the Middle Eocene and the lower part of the Upper Eocene (Curry *et al.* 1969). Although none of the proposed microplankton zone boundaries corresponds exactly with the major stratigraphical boundaries suggested by Curry *et al.* (1969), broadly speaking the upper part of the Lower Eocene is represented by microplankton Zones 1 and 2, the Middle Eocene by Zones 3 and 4, and the lower part of the Upper Eocene by Zone 5 (Fig. 29).

This zonal scheme is essentially for local application, but the major palynostratigraphical trends shown by the microplankton assemblages should be recognizable over a much wider geographical area.

b. *Correlation of the Bracklesham Beds at Whitecliff Bay and Alum Bay*

The Bracklesham Beds at Whitecliff Bay and Alum Bay have never been satisfactorily correlated because of the considerable contrast in lithological sequence between the two and the absence of marine faunas at Alum Bay from all but the highest part of the sequence (Eaton 1971b : text-fig. 1). The record of microplankton assemblages through most of the Bracklesham Beds at Whitecliff Bay and in four intervals in the sequence at Alum Bay allows the two sections to be correlated.

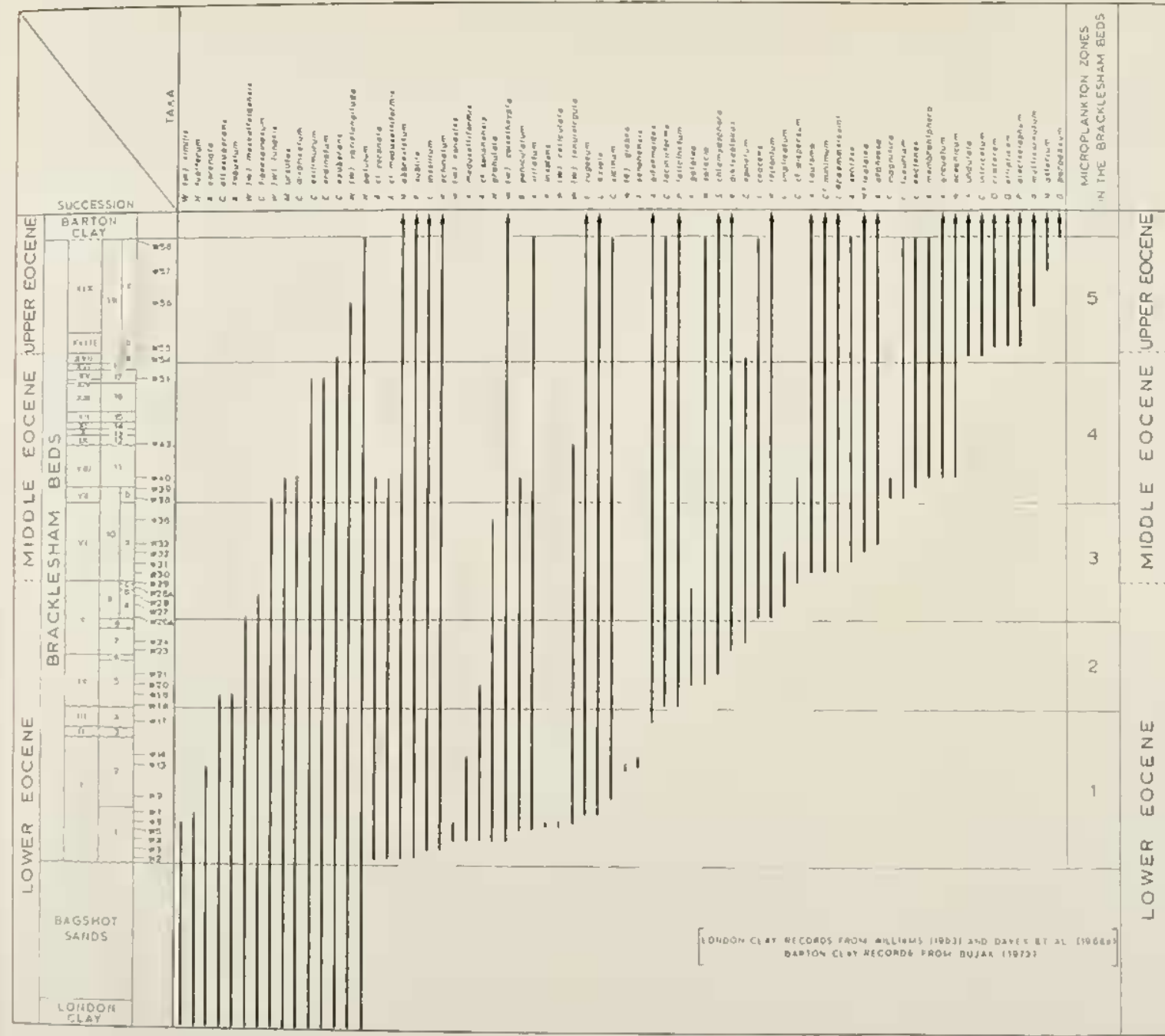
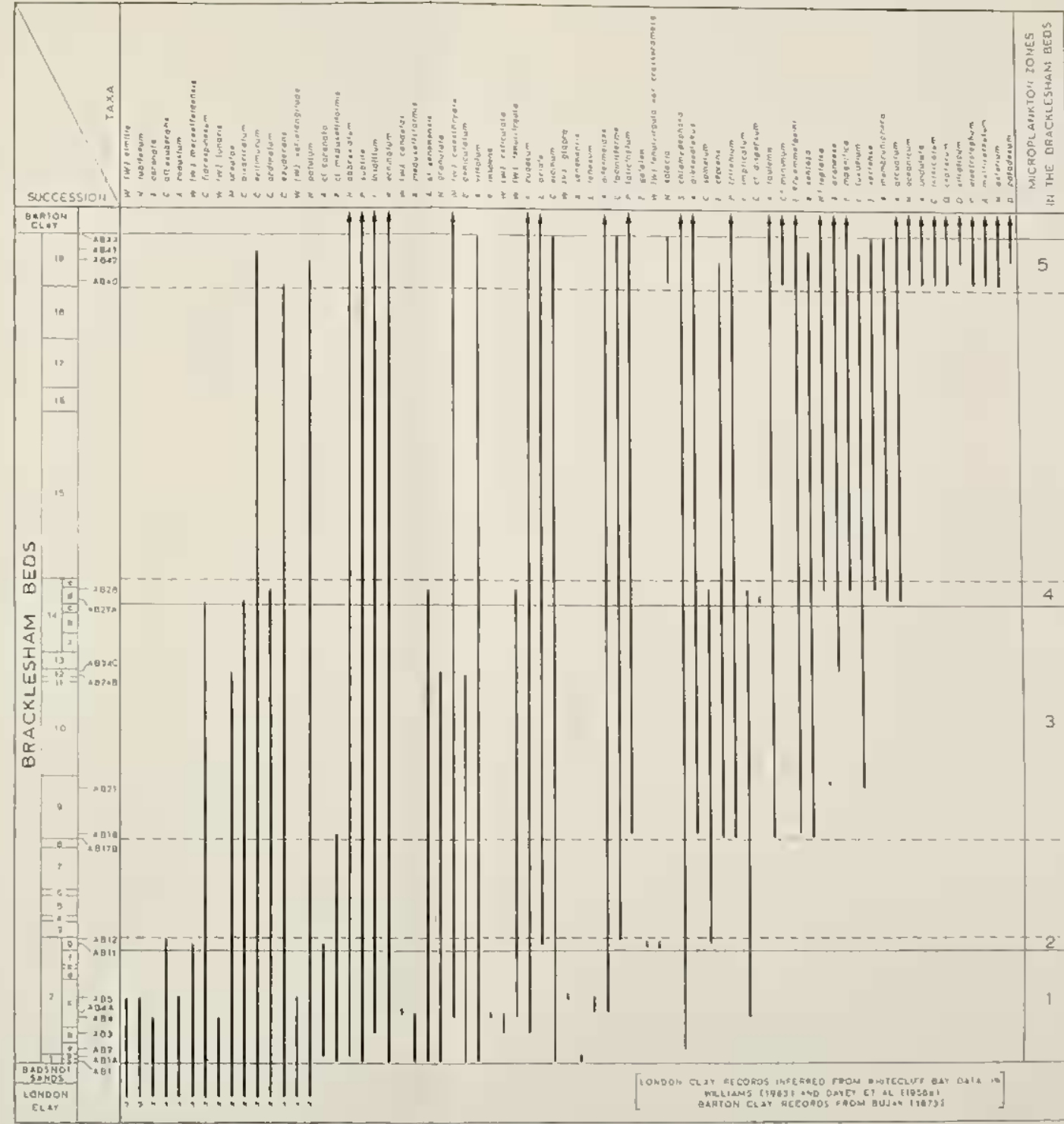


FIG. 29 Stratigraphical ranges of selected dinoflagellate cyst taxa in the Bracklesham Beds at Whitecliff Bay, Isle of Wight.



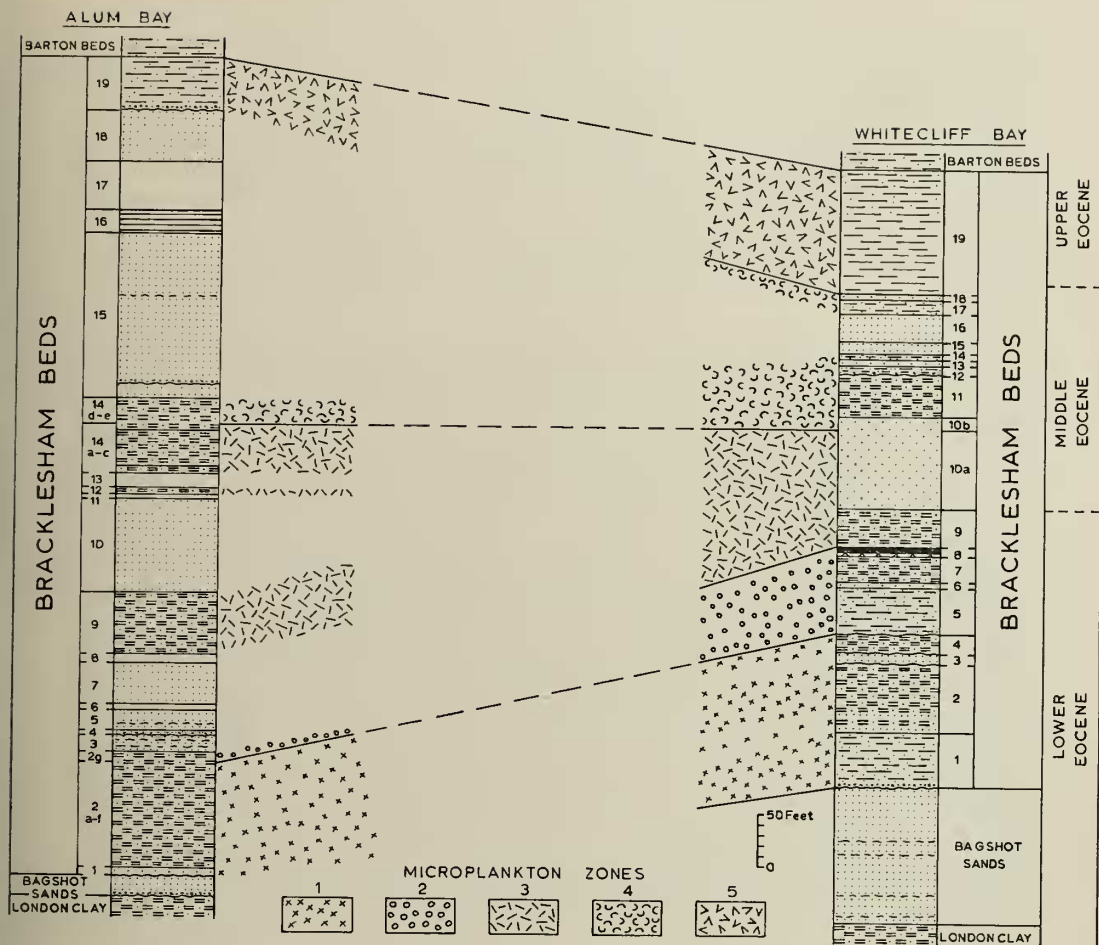


FIG. 31. Comparative distribution of the five microplankton zones in the Bracklesham Beds at Whitecliff Bay and Alum Bay, Isle of Wight.

The comparative distribution of the five microplankton zones in the two sections is shown in Fig. 31. The diagram in Eaton (1971a : text-fig. 2 ; 1971b : text-fig. 1) indicates that all four interzonal boundaries defined at Whitecliff Bay are recognizable at Alum Bay. Using purely palynological data only the 1/2 and 3/4 zone boundaries can be recognized. Strictly speaking the horizon marking the 4/5 zone boundary cannot be defined at Alum Bay, but using all available geological data there are strong indications that the horizon representing the 2/3 zone boundary at Whitecliff Bay does correlate with the boundary between beds 3 and 4 at Alum Bay.

The sequence of sands and pipeclays (bed 3–bed 8) previously assigned to the Bagshot Sands at Alum Bay (White 1921) are correlated with the upper part of Zone 2 and the lower part of Zone 3 of the Bracklesham Beds at Whitecliff Bay (the sediments associated with the lignite bed, bed 8). The underlying laminated beds and sands at Alum Bay (bed 1a–bed 2g), which have been previously assigned to the London Clay (White 1921), are correlated with Zone 1 and the lower part of Zone 2 of the Bracklesham Beds at Whitecliff Bay. This possibility was suggested by Curry (in Wright & Curry 1959 : 14).

c. *Comparison with microplankton assemblages from the Lower Eocene of the London Basin*

On the north Kent coast in south-east England the Bracklesham Beds are not represented, and the Lower Eocene London Clay is succeeded only by the Bagshot Sands. Microplankton have been described from the London Clay of this area by Williams (1963) and Husain (1967), and the results of their work have been published in Davey *et al.* (1966a) and Downie, Husain & Williams (1971).

Several dinoflagellate cysts which appear in the lowest Bracklesham Beds (microplankton Zone 1) of the Isle of Wight have been noted in the London Clay of north Kent. *Wetzeliiella* (W.) *tenuivirgula* persists throughout the London Clay in this area, *Eocladopyxis peniculatum*, *Impletosphaeridium implicatum*, *I. rugosum* and ? *Phthanoperidinium echinatum* are present in the lower part of the London Clay, and *Polysphaeridium subtile*, *Wetzeliiella* (R.) *glabra*, *Wetzeliiella* (W.) *condylos* and *W. (W.) reticulata* are present in the upper part of the London Clay. Although these records do not indicate a simple, straightforward stratigraphical relationship between the microplankton assemblages from the Lower Eocene of the Hampshire and London Basins, the restricted distribution of *P. subtile*, *W. (R.) glabra*, *W. (W.) condylos* and *W. (W.) reticulata* suggests that the upper part of the London Clay in north Kent may be younger than the London Clay of the Isle of Wight.

Although microplankton have proved effective for correlating the Bracklesham Beds of the Isle of Wight, considerably more palynological data are required from the northern part of the Hampshire Basin and the western part of the London Basin before the Lower Eocene sediments in southern England can be precisely correlated using microplankton assemblages.

V. COMPARISONS WITH PREVIOUS STUDIES OF EOCENE MICROPLANKTON IN NORTHERN EUROPE

In this section emphasis is placed on studies of Eocene microplankton which have yielded taxa considered to be stratigraphically significant in the Bracklesham Beds of the Isle of Wight.

a. *Belgium*

De Coninck (1968, 1972) described microplankton assemblages from Lower Eocene sediments in a borehole at Kallo near Antwerp. This penetrated (in descending order) Belgian representatives of the Cuisian Argile de Merelbeke (Paniselian)

and Sables de Mons-en-Pévèle, and the Sparnacian (in the sense of Curry *et al.* (1969)) Argile d'Ypres.

The stratigraphical appearance of *Homotryblium abbreviatum* (as *Hystrichosphaeridium tubiferum brevispinum*), *Samlandia chlamydophora* and possibly *Achilleodinium biformoides* (as *Hystrichokolpoma ? biformoides*) in the highest 25 metres of the Argile d'Ypres, and of *Areosphaeridium diktyoplokus* in the Argile de Merelbeke, parallels the distribution of these species in microplankton Zones 1 and 2 of the Bracklesham Beds. The possibility of the highest part of the Argile d'Ypres at Kallo being younger than the London Clay of southern England is also indicated by a comparison of the microplankton associations from the two areas (Downie, Husain & Williams 1971 : 34).

Isolated assemblages from the Argile d'Ypres at Langemark, Kortemark and St Jan have been studied by Morgenroth (1966a) and yielded *Achilleodinium biformoides*, *Lanternosphaeridium lanosum*, *Samlandia chlamydophora* and *Wetzelietta* (R.) *glabra*. The presence of these species suggests a comparison with the highest part of the Argile d'Ypres at Kallo, and microplankton Zone 1 of the Bracklesham Beds.

b. North Germany

There are five divisions in the German Eocene : Lower Eocene 1-4, and Upper Eocene. Lower Eocene divisions 1-3 are considered to be equivalent to the Lower Eocene of the Anglo-Paris-Belgian Basin, and the Middle Eocene is represented by the German Lower Eocene 4.

For comparison with the microplankton assemblages from the Bracklesham Beds, the most significant work on the German Eocene is that of Morgenroth (1966a). He described assemblages from the Tarras (the 'equivalent' of the London Clay in north Germany) on Fehmarn Island. The Tarras has been variously assigned to Lower Eocene 4, Lower Eocene 3/4, and Lower Eocene 2. The rich microplankton assemblages from this lithostratigraphical unit include *Achilleodinium biformoides*, *Adnatosphaeridium robustum*, *Areosphaeridium diktyoplokus*, *Cordosphaeridium ? minimum*, *Eocladopyxis peniculatum*, *Impletosphaeridium implicatum*, *I. kroemmelbeini*, *I. rugosum*, *Lanternosphaeridium axiale*, *L. lanosum* and *Samlandia chlamydophora*.

C. ? minimum and *I. kroemmelbeini* were not recorded below microplankton Zone 3 in the Bracklesham Beds. The specimen of *A. diktyoplokus* figured by Morgenroth (1966a : pl. 4, figs 11-12) is comparable to the earliest representatives of this species recorded in Zones 2 and 3 (Eaton 1971a : pl. 1, fig. 3). *A. robustum* was only recorded in Zones 1 and 2, and *L. lanosum* only in Zone 1 of the Bracklesham Beds. The other six significant species first appear in Zone 1 and persist through Zones 2 and 3.

Although several key species are absent, direct comparison between the north German assemblages and those from the Bracklesham Beds suggests that the Tarras includes representatives of microplankton Zones 1, 2 and 3, i.e. the upper part of the Lower Eocene and possibly the lowest part of the Middle Eocene.

Agelopoulos (1967) described assemblages from Middle and Upper Eocene sediments at Heiligenhafen, north Germany. The Middle Eocene assemblages include

Areosphaeridium diktyoplokus, and this species was also recorded in the Upper Eocene together with *Achilleodinium biformoides*, *Achomosphaera membraniphora* and *Samlandia chlamydophora*. In the Bracklesham Beds these species were recorded in the Upper, Middle and (*A. membraniphora* apart) Lower Eocene.

Gocht (1969) described assemblages from Palaeocene, Lower, Middle and ? Upper Eocene, and Middle Oligocene sediments in two boreholes at Meckelfeld near Hamburg, north Germany. The majority of the assemblages are dominated by *Cordosphaeridium* (*C. inodes* and *C. gracilis*), allowing little comparison with the assemblages from the Bracklesham Beds. It is significant, however, that Gocht noted the persistence of the *Areoligera senonensis* complex into the Middle Eocene, as is the case in the Bracklesham Beds.

c. Northern France

Microplankton assemblages recorded from the Eocene of northern France include only a few of the species which are considered to be stratigraphically important in the Bracklesham Beds. The most significant assemblages are those described from the Lower Eocene (Cuisian) Varengeville Formation in Normandy by Gruas-Cavagnetto (1970b). The *Areoligera senonensis* complex forms a prominent part of the assemblages, in association with *Hystriosphæridium tubiferum* and *Impletosphæridium implicatum* (as *Adnatosphaeridium* ? *capilatum*). This suggests a comparison with microplankton Zone 1 of the Bracklesham Beds.

VI. PALYNOSTRATIGRAPHICAL SUMMARY

The potential stratigraphical value of microplankton for correlation in the Eocene of southern England and northern Europe has been demonstrated in sections IV and V of this paper. The most significant palynostratigraphical features of the assemblages encountered in the present study are listed here.

1. The appearance of the genera *Achilleodinium*, *Pentadinium*, *Samlandia* and *Turbiosphaera* in the upper part of the Lower Eocene, *Araneosphaera* in the Middle Eocene, and the appearance and diversification at specific level of *Diatodinium* in the lower part of the Upper Eocene.
2. The diversification at specific level of *Phthanoperidinium* through the Eocene.
3. The appearance of *Areosphaeridium* in the upper part of the Lower Eocene, and its diversification at specific level through the Middle and Upper Eocene.
4. The decline of the *Areoligera senonensis* complex in the Middle Eocene, and its stratigraphical 'replacement' by species with more membranous processes (*A. sentosa*, *A. tauloma*, *A. undulata*).

The microplankton assemblages which have been described from Palaeogene sediments in Europe and other parts of the world frequently only include the more common stratigraphically long-ranging taxa, or they are dominated by forms of apparently restricted geographical distribution. Fortunately, as indicated below, there are records of the morphologically more distinctive taxa considered to be stratigraphically significant in this study, in assemblages other than those discussed in section V.

The most notable of these taxa is *Areosphaeridium*. *A. diktyoplokus* has been recorded from the Tertiary of Europe (Belgium, England, north Germany, Norwegian North Sea, East Prussia, Romania), North America (Aleutian Islands), South America (Argentina including Tierra del Fuego, Chile) and Antarctica. Some of these records are from undifferentiated Tertiary sediments, but there are indications of a stratigraphical range from Lower Eocene to Miocene with particular emphasis on the Eocene.

The only area in which Palaeogene microplankton have been studied in some detail without yielding *A. diktyoplokus* is Australasia, although it has been recorded as a reworked form in the Pleistocene of New Zealand (Wilson 1973). This apparent absence is all the more surprising when it is considered that forms probably referable to *Areosphaeridium* have been recorded from the Upper Eocene of Victoria, Australia – as *Cordosphaeridium capricornum* Cookson & Eisenack 1965 (Eaton 1971a: 364).

Areosphaeridium arcuatum and *A. multicornutum* have only been recorded from the Middle and Upper Eocene and from the Upper Eocene, respectively, of southern England, but other records of forms probably attributable to *Areosphaeridium* include *Baltisphaeridium pectiniforme* from the Middle Oligocene (Gerlach 1961; Benedek 1972, as *Cleistosphaeridium pectiniforme*) and Upper Oligocene (Brosius 1963) of north Germany, and '*Baltisphaeridium*' cf. *B. pectiniforme* from the Upper Eocene of the Aleutian Islands, north Pacific Ocean (Evitt 1970). The inception of *Areosphaeridium* in the Eocene and its diversification at specific level through the Eocene and Oligocene appear to be a world-wide feature of Palaeogene microplankton assemblages.

Three species of *Phthanoperidinium* were recorded from the Bracklesham Beds (*P. alectrophum*, *P. echinatum*, *P. tritonium*). Representatives of this genus are also known from the Palaeocene and the Lower Eocene of northern France (Chateau-neuf & Gruas-Cavagnetto 1968, *P. resistente*), the Lower Eocene of north Germany (Morgenroth 1966a, *P. resistente*) and northern Spain (Caro 1973, *P. campoense*), and the Upper Eocene of Victoria, Australia (Cookson & Eisenack 1965, *P. eocenicum*). The persistence of *Phthanoperidinium* into the Oligocene is indicated by records from the Lower Oligocene of north Germany (Morgenroth 1966b, *P. comatum*) and the Oligocene of Mississippi, U.S.A. (Drugg & Loeblich 1967, *P. amoenum*).

Distatodinium is represented by three species in the Upper Eocene part of the Bracklesham Beds (*D. craterum*, *D. ellipticum*, *D. paradoxum*), but published records suggest that this genus is more characteristic of the Oligocene, particularly in Europe. *D. craterum* has been recorded from the Middle Oligocene of Switzerland (Scherer 1961, as *Hystriospheraidea*), *D. ellipticum* and *D. tenerum* from the Middle and Upper Oligocene of north Germany (Benedek 1972), and *D. paradoxum* from the Middle Oligocene (Gocht 1969, Benedek 1972) and Upper Oligocene (Brosius 1963, Benedek 1972) of north Germany. *D. ellipticum* is also known from the Upper Eocene of Victoria, Australia (Cookson 1965).

The trend towards marginate cyst taxa with more membranous processes, indicated by the stratigraphical 'replacement' of the *Areoligera senonensis* complex by *Areoligera sentosa*, *A. tauloma* and *A. undulata* through the Middle Eocene, is

emphasized by the appearance of *Chiropteridium* cf. *dispersum*, *Cyclonephelium laciniiforme* and *C. spinetum* in the upper part of the Lower Eocene and the Middle Eocene.

A. undulata, which was found to be very common in the Upper Eocene in this study, has also been recorded by Eisenack (1954, as *Palmnickia* sp. indet.) from the Bernstein Formation in the Samland area of East Prussia (now Russia). This formation was then considered to represent the Lower Oligocene, but Eisenack later (1965) assigned it to the Upper Eocene. The persistence and diversification of membranous-processed marginate cyst taxa into the Oligocene are confirmed in microplankton studies of material from north Germany: e.g. Gerlach (1961), Brosius (1963), Gocht (1969) and Benedek (1972).

These records of morphologically distinctive, stratigraphically significant taxa from sediments in widely separated parts of the world hold out considerable hope for the application of microplankton to long range stratigraphical correlation in the Palaeogene.

VII. ACKNOWLEDGEMENTS

This research was carried out during the tenure of an N.E.R.C. Studentship in the Department of Geology, the University of Sheffield.

I gratefully acknowledge the advice and assistance of Dr C. Downie in his supervision of this work. Thanks are also due to Professor L. R. Moore for allowing full use of facilities in the Department of Geology, to the British Petroleum Co. Ltd for technical facilities in the Exploration and Production Research Division of the BP Research Centre at Sunbury-on-Thames, to Mrs M. E. Clack for typing the manuscript, and to Mr C. J. H. Simmonds for his assistance with the photography.

I am grateful to Dr J. Bujak for allowing me to use data from his unpublished Ph.D. thesis.

Finally, I wish to thank my wife for her constant help and encouragement during the preparation of this paper.

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